Blink-contingent object displacements during tracking: behavioural and neuromagnetic recordings

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ABSTRACT OF THE
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The visual world is perceived as continuous despite frequent interruptions of sensory data due to eyeblinks and rapid eye movements. To create the perception of constancy, the brain makes use of fill-in mechanisms. This study presents an experiment in which the location of an object during smooth pursuit tracking is altered during eyeblinks. The experiment investigates the effects of blink suppression and fill-in mechanisms to cloud the discrimination of these changes. We employed a motion-tracking task, which promotes the accurate evaluation of the object's trajectory and thus can counteract the fill-in mechanisms. Six subjects took part in the experiment, during which they were asked to report any perceived anomalies in the trajectory. Eye movements were monitored with a video-based tracking and brain responses with simultaneous MEG recordings. Discrimination success was found to depend on the direction of the displacement, and was significantly modulated by prior knowledge of the triggered effect. Eye-movement data were congruent with previous findings and revealed a smooth transition from blink recovery to object locating. MEG recordings were analysed for condition-dependent evoked and induced responses; however, intersubject variability was too large for drawing clear conclusions regarding the brain basis of the fill-in mechanisms.

Keywords: blinking, real-time blink detection, visual discrimination, blink suppression, MEG, human visual cortex, eye tracking, motion perception, smooth pursuit eye movements, visual stability

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Visuaalinen maailma koetaan jatkuvana, vaikka silmänräpäykset ja nopeat silmänliikkeet aiheuttavat keskeytyksiä sensoriseen tiedonkeruuseen. Luodakseen käsityksen pysyvyydestä, aivot käyttävät täyttömekanismeja. Tämä tutkimus esittelee kokeen, jossa kappaleen seurantaa hitailla seurantaliikkeillä häiritään muuttamalla sen sijaintia silmänräpäysten aikana. Tämä koe tutkii, kuinka silmänräpäysten aiheuttama suppressio ja täyttömekanismit sumentavat kykyä erotella näitä muutoksia. Käytimme liikeseurantatehtävää, joka vastaavasti edistää kappaleen liikeradan tarkkaa arviointia. Kuusi koehenkilöä osallistui kokeeseen, jonka aikana heitä pyydettiin ilmoittamaan kaikki havaitut poikkeamat kappaleen liikeradassa. Silmänliikkeitä tallennettiin videopohjaisella seurannalla, ja aivovasteita yhtäaikaisella MEG:llä. Erottelykyvyn todettiin riippuvan poikkeutuksen suunnasta, sekä merkittävästi a priori tiedosta poikkeutusten esiintymistavasta. Silmänliikedata oli yhtenevää aiempien tutkimusten kanssa, ja paljasti sujuvan siirtymisen silmänräpäyksistä palautumisesta kappaleen paikallistamiseen. MEG-tallenteet analysoitiin ehdollisten heräte- ja indusoitujen vasteiden löytämiseksi, mutta yksilölliset vaste-erot koehenkilöiden välillä olivat liian suuria selkeiden johtopäätösten tekemiseksi täyttömekanismien aivoperustasta.

Avainsanat: silmänräpäys, reaaliaikainen silmänräpäytysten tunnistaminen, visuaalinen erottelukyky, silmänräpäysten aiheuttama suppressio, MEG, näköaivokuori, silmänliikkeiden seuranta, liikkeen havainnointi, silmien hitaat seurantaliikkeet, visuaalinen stabiliteetti

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1 Introduction

While a blink of the eyes might seem a trivial event, from the perspective of the visual system, it effectively means losing accurate sensory input for nearly half a second. The timeframe may appear negligible at face value, as blinks usually come and go unnoticed, yet at the time scale of perception and neural processing, much happens. In comparison, humans and other animals are able to execute delicate visuomotor manoeuvres requiring temporal precision in the range of tens of milliseconds [1]. Despite that, the ability to estimate a time interval is interestingly not as accurate, and varies greatly by task [2, 3]. Time perception remains, for both sub-second and extended time ranges, largely unresolved to this date. While several key brain areas regarding the ability to measure time have been identified, questions remain about the nature of the underlying mechanisms and how temporal information is integrated into sensory information [4, 5].

A scenario such as eyeblinks occurs only for sight, and it would indeed be bizarre to imagine our other senses being affected by such gaps in incoming information on a regular basis. Nevertheless, it would appear logical that there is a neural mechanism to stabilize our perception of our visual surroundings such that it remains stable, and the research reviewed in this thesis supports this idea by both neural and behavioural observations. It is known that activity in the visual cortex is suppressed during blinks as well as saccades, rapid eye movements [6, 7]. Evidence points towards neural pathways between the visual cortex and oculomotor regions, suggesting that processing of visual information is modulated by eyelid and eye orientation [8]. While a seemingly effective means of filtering out inaccurate, distracting information [9], this movement-induced suppression also means that our ability to detect changes occurring during these intervals is surprisingly poor [10].

Additionally, this begs the question of how the image is kept in memory for the duration of the blink, and how the perception of a stable world is maintained. As neural activity is significantly lowered, such a model cannot depend on continuous sensory feedback. Maintaining an impression of continuity, that is to say, to predict the position of objects due to their or the observer's motion during blinks and other gaps in input, necessitates both being able to maintain memory of the visual scene at the onset of a blink and approximate the time that has passed during a blink. On the other hand, the visual system is keen to produce the sense of continuity via illusory perceptions, especially when retinal input is impaired, as it can be argued that little functional gain comes from explicitly identifying changes that might occur during blinks [11, 12].

Investigating motion tracking reveals that predicting the trajectory of a target, e.g. in preparation of catching a ball, is less reliant on immediate sensory information, and more on the internal representation of the object, which in turn is based on previous data and expected behaviour [13, 14]. This approach corresponds well with the frequency of aforementioned discontinuities in sensory input. However, a further question remains about the nature of mechanisms that supposedly maintain this image in memory, and to what extent this information is applied [15]. The visual system does not record the observed world objectively and uniformly like a video camera, but rather the perceived scene integrates sensory input with preconceptions of spatial and temporal patterns [11, 16]. Thus, it cannot be ascertained that visual continuity is simply a result of fastidious evaluation of time and scenic memory rather

than a combination of those factors and fill-in mechanisms. Likely, a threshold between the two exists, where the observer would recognize large enough discontinuities should they occur.

All in all, eyeblinks incorporate these interesting aspects of cognitive processing – time perception, smoothing gaps or flaws in sensory input, and predicting object locations – in an ostensibly simple routine. Regardless, blinks are in most cases considered a hindrance rather than a research interest, on account of the related eye and muscle movements confounding electromagnetic signals arising from the brain, as well as possibly interfering with presenting visual stimuli. Blink-contaminated trials are often discarded, leading to data loss and longer measurement sessions. However, as technology has improved, so has the ability and interest to examine transient events such as blinks; yet, the rapid nature of these events remains a challenge. Voluntary or reflex blinks can be elicited by instructions or sensory cues, respectively, to use in experiments, with the caveat that an automated setup might still require the subject to time his or her actions just right, and the delicate timing must still be verified in post-processing [7]. Correspondingly, the unpredictable nature of spontaneous blinks demands high-resolution real-time monitoring in order to incorporate their timing to an experiment in a meaningful way.

Investigating blink-related brain activity does amplify the issue of nuisance signals related to the act of blinking, since they would be very closely time-locked to the investigated neural activity, and thus challenging to remove completely. While cognitive processing operates with a delay of at least some tens of milliseconds due to signal propagation times, any activity elicited by cognitive processing of stimuli appearing during a blink should be detectable after blink-related artefacts have vanished [17]. Yet, the sheer magnitude of blink artefacts can be troublesome in analysing the time frames of interest. Additionally, the simple change in retinal illumination at the offset of a blink will obviously produce a strong but predictable response by itself, which might confound any particular activity. Thus, the blink-contingent paradigm presents unique challenges in both experimental setup and post-processing of the data.

This thesis introduces an experimental procedure that, in essence, tries to be faster than the eye to examine blink-related brain activity. Often, a simple way to assess a system is to introduce a flaw in its workings and observe the consequences. In this experiment, the tracking of a predictably moving object on screen is disturbed by changing its position along the foreseeable trajectory during spontaneous blinks. The purpose of the experiment is determining how manipulating visual stimuli during eyeblinks is perceived by the subject, with the main focus being the contradicting effects between fill-in and object-tracking mechanisms.

By varying the magnitude of the displacement, the scheme is used to determine a threshold where the subjects fail to notice the blink-concurrent manipulation, and whether crossing the threshold results in differing eye movements or neural activity. The temporal finesse required to perform such an experiment has been possible and advanced on previously [18], and the goal of the study is not to improve the technology but rather to apply a blink-contingent research model to an existing setup. Nevertheless, the experiment breaks into scarcely researched territory by focusing on spontaneous blinks. Compared to reflex or voluntary blinks, the scenario may elicit a more natural reaction (insofar as the monitoring setup allows), as it does not employ a blink-triggering stimulus. To the author's knowledge, the combination of blink-related visual suppression and a moving target has not been used to this effect, and the results

will likely provide new insight into the inner workings of visual fill-in mechanisms and motion perception.

In this thesis, in addition to acquiring subjects' reports about their perception, our combination of a magnetoencephalographic (MEG) device and an infrared eye tracker camera allowed for gathering eye-movement data to monitor for blinks and post-blink gaze patterns and electromagnetic brain signals to study stimulus-evoked activity. Both of them can reveal important details about the transient reactions to the object displacement. Importantly, these two devices provide information with millisecond temporal resolution, thus the timing requirement falls most heavily on the stimulus presentation system to both react to blinks in real time and present changes in the visual stimulus sufficiently fast. These challenges in timing are discussed throughout the thesis, as well as the background of relevant theories about vision and the neural mechanics outlined above, with the aim of providing insight and guidance in setting up the experimental procedure. Finally, the results of conducting the experiment are presented and their relation to the theories evaluated.

2 Background

This section provides the basis for understanding the phenomena investigated and the means of monitoring employed in the experimental setup.

2.1 Non-invasive monitoring of human brain function

There are on the order of 10^{10} neurons in the brain, forming approximately 10^{14} synaptic – excitatory or inhibitory – connections with each other [19]. Within a neuron, information is sent out as action potentials, self-propagating impulses during which the membrane potential of the cell changes rapidly due to ionic concentration differences across the membrane and the opening of voltage-gated ion-specific channels [20]. In synapses, the action potential is relayed between neurons with neurotransmitter chemicals, which when binding to the receptors of the post-synaptic cell change the local ion permeability – and thus the membrane potential – of the cell, triggering ion flows across the membrane. Given sufficient excitatory stimulation, depending on inbound action-potential frequency, to shift the membrane potential beyond the needed threshold, the action potential begins to propagate in the postsynaptic cell.

While the electromagnetic fields arising from a single neuron are exceedingly small when measured external to the head, the organization of neurons into large structures recruited to a common task can produce a noticeable signal to a sensor outside the skull. Action potentials themselves are too brief to effectively summate, as the largest amplitude phase lasts for one or two milliseconds, with a similar refractory period. On the other hand, *postsynaptic potentials* (PSPs) from the aforementioned ionic currents can last around 10 ms or more, which is a sufficient time window to cause the superimposed signals stemming from mass activity to be directly detected by external means [21].

2.1.1 Magnetoencephalography

Magnetoencephalography (MEG) is the method of choice in this thesis. MEG directly measures the magnetic fields caused by clusters of PSP-related currents, and does it with a sampling rate usually in the region of 1000 Hz, meaning any activity is seen on the sensors nearly instantaneously and with a temporal resolution well in line with the underlying neural signalling [22]. Its spatial resolution, however, is somewhat limited due to the ill-posed inverse problem and the weakness of the induced magnetic fields.

Furthermore, the detectability of a MEG signal source depends greatly on its location and orientation. The more radial the source, i.e. current dipole is pointing outward/inward from the centre of the head, the lower the amplitude of its externally visible magnetic field [23] – though perfectly ill-oriented sources are improbable, and attenuation as a function of orientation is taken into account in source localization [24]. However, the lower amplitude of signals of interest means poorer signal-to-noise ratio (SNR). Additionally, from the perspective of the detectors, radiality applies with increasing significance to sources far from the surface. This makes activity from deep-lying sources increasingly difficult to detect, as they would already produce weaker signals at the detectors due to increased distance between them. In practice, the sensitivity dependencies imply that MEG is mainly sensitive to signals from neuron clusters

aligned parallel to the skull, i.e. are located in fissures and sulci of the cortex [21]. The well-detectable area includes e.g. the visual as well as all other primary sensory areas, and source estimation is indeed often limited to the cortex. However, recent studies have also found success in using MEG to map activity in deep brain structures such as the hippocampus [25] and brainstem [26].

Analysing the sensitivity of MEG w.r.t. the signal sources, a single excitatory PSP generates a transient magnetic dipole of some tenths of a pico-ampere-meters (fAm) [27]. In order to pick up these signals, the MEG measuring unit employs helmet-shaped array, consisting of several highly sensitive *superconductive quantum interference devices* (SQUIDs). The SQUIDs are able to detect magnetic fields with magnitudes as low as 5 femto-teslas arising from the brain, which corresponds to an approximate source dipole strength of 10 nAm [27]. Given the aforementioned contribution of a single synapse, such a source strength represents the cumulative activity of millions. In addition, considering the summation of signals will not be ideal due to disparately aligned synapses partially cancelling the fields of one another, and only a small portion of a neuron population in the brain would realistically fire action potentials simultaneously, the corresponding area of cortex necessary to produce detectable signals would be some tens of square millimetres, further depending on assumptions on e.g. effective depth [21, 22].

As the fields arising from neural activity are extremely weak, any external interference, from for example traffic and elevators, will be several orders of magnitude greater and thus render the sensor information useless (Figure 1). Because of this, MEG necessitates using a highly effective magnetically shielded room in which to conduct measurements, and obviously any additional equipment used for an experiment must be compatible with this setup [28]. In addition to external noise, other sources of magnetic fields inside the body, most notably muscles, also produce significant signals to MEG sensors, which must be filtered out [29, 30].

Additionally, in order to obtain useful information about the neural response to an event, the activity evoked by the stimulus must be distinguished from on-going spontaneous neural activity. While data from a single stimulus presentation will not reveal any differences between the two, averaging gathered data across multiple stimulus repeats will gradually cancel out random activity as well as other noise present in the recordings. As the activity elicited by the stimulus is often considered to remain similar across repeats, any irregular signal components are effectively attenuated by the process. Averaging the signal over the relevant time window increases its SNR proportional to the square root of the number of repeats, in practice necessitating that stimuli are repeated around 100 times (see for example Ref. [31]). This process is required with any technique of functional brain imaging, but as MEG has a poor initial SNR, the necessary amount of repetition for the event-related fields to be robustly detectable is relatively high. For the experiment in this thesis, averaging is slightly more challenging, as the responses of interest are to a spontaneous event. In the more common scenario, one can time-lock the temporal window of interest to the predetermined event of stimulus onset (e.g. an image is presented), which is not as well-determined in this case. This problem is analysed more thoroughly in Chapter 3.

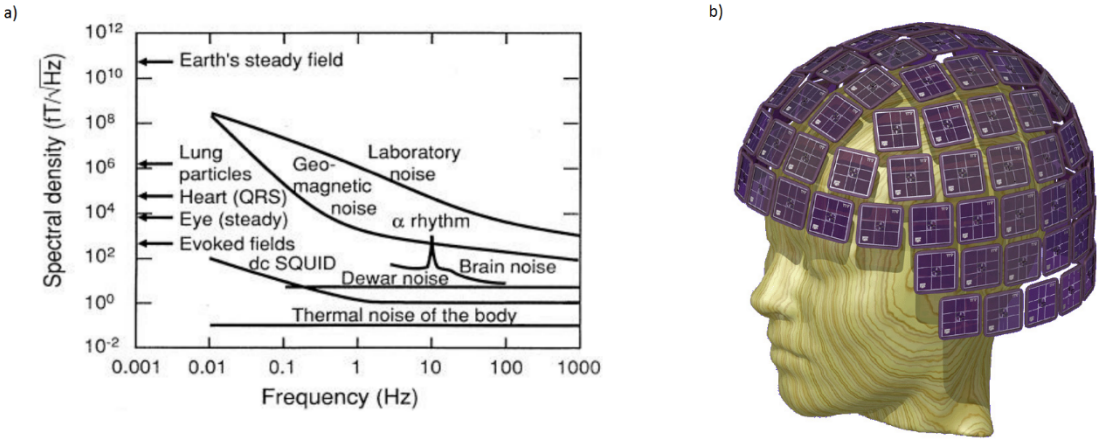

Figure 1 – a) The magnitude of event-related signals compared to unwanted noise source [21]. b) Typical SQUID sensor array formation in a MEG device (image: ltl.aalto.fi)

2.1.2 Other methods of detecting neural activity

Electroencephalography (EEG) is the electric counterpart to MEG, and thus a good point of comparison. Both similarly measure the direct electromagnetic activity with great temporal resolution, but important distinctions exist between the two. EEG is a well-established technique in both basic research and clinical studies that has been conducted for nearly a century. One of the advantages of EEG is that technologically it is far less demanding than MEG. Electric signals are gathered using electrodes in contact with the scalp of the subject, where signal amplitudes of neural sources typically ranging from 10 to 100 μV, meaning there is no need for ultra-sensitive sensors. While regular noise sources will still cause disturbances in the millivolt range, and thus necessitate post-processing of data, the measurements can still take place in an ordinary room, allowing more flexibility in experiment design as well as being significantly cheaper by not requiring additional shielding.

In comparison to MEG, where magnetic fields are relatively unaltered by tissues they propagate through, the electric signals EEG measures are affected by the conductivity of head tissues [32]. Furthermore, upon reaching the scalp, the electric currents continue to conduct along its surface to nearby electrodes, producing a smear effect in the signal. This decreases the spatial resolution of EEG. EEG and MEG are also complementarily sensitive to sources w.r.t. their orientation. Where radial sources generate signals that are poorly receivable by MEG, EEG is most sensitive to radial sources. Of the two, EEG is overall significantly less affected by source orientation [33], while both methods have poor resolution for deep-brain sources.

Indirect methods for monitoring neural activity can also be employed, with the most prominent techniques being positron emission tomography (PET) and functional magnetic resonance imaging (fMRI). These methods aim to detect changes in metabolism caused by neurons firing action potentials, on the basis that the process exhausts resources from the cell. Thus, the latency and the magnitude of a replenishment response can be corresponded with transpired brain activity, with the caveat that the true correlation between the two may not be straightforward. In the case of fMRI, the idea is to detect local changes in cerebral blood flow, as oxygenated blood flow to active areas increases [34]. PET on the other hand monitors the

decay of injected radioactive, metabolically-active molecules (e.g. glucose analogues), which will have the highest concentrations in active sites [35]. While the necessary radiation dose for PET is similar to a computed tomography scan, it may discourage use for purely research interests in humans. Additionally, neither technique presents a very natural or adjustable situation for the subject due to the necessary equipment, and in the case of fMRI, the subject being constrained inside a powerful and acoustically noisy magnet causes further restrictions to the experiment setup.

Compared to electromagnetic techniques, these methods have superior spatial resolution of circa 2 mm, and importantly the precision is similar throughout the brain [22]. The results can also easily be superimposed with e.g. a regular MRI image to match the activity accurately to anatomical structures. Additionally, significant results can be attained with fewer stimulus repeats as MEG [see 33], but the total time required for the measurement may still be equal or greater. However, as the metabolic processes are slow and happen with a delay of some seconds after the activity of interest, the temporal resolution of these methods remains low at approx. 1 s for fMRI and nearly a minute for PET [22, 37]. This can be worked around to an extent, for example Onoe et al. [35] limited the recording to a smaller timeframe of interest at the cost of lengthy measurement sessions. These indirect methods would fit poorly to an experiment such as the one presented here due to their inability to discern the rapid neural processes taking place, with blinks and the following related activity will all transpire in less than a second.

While transcranial magnetic stimulation (TMS) does not by itself produce metrics of brain activity, it can be used to gain insight on the topic by inducing electrical currents in the brain and monitoring their behavioural effects, and it is employed in some of the studies reviewed here to great effect. This stimulation can be either excitatory or inhibitory; e.g. in the case of targeting the motor cortex, TMS can produce muscle movements or suppress them with a brief (sub-millisecond) and otherwise harmless magnetic pulse [38]. Moreover, the effects of the pulse are limited very accurately in both time (ca. 50 to 250 ms) and location (a few millimetres depending on instrumentation) [17, 39, 40]. Thus, it is possible to identify key functional areas of the brain by stimulating them at specific periods of time, and observing the resulting performance changes in an experiment task. Targeting the visual cortex, TMS can be used to induce sensations of light (phosphenes), diminished visual acuity or inability in functions such as motion processing [17].

2.2 Human visual system

The human visual system consists mainly of the eyes, the occipital lobe, and the pathway that delivers information from the eyes to the occipital cortex as well as other hubs. In this section, the above basis of neural signal generation is expanded on, in order to explain the roles of functional areas in processing visual information. Additionally, the physiology of eye movements and eyeblinks is reviewed for the eye movement analysis part of the introduced experiment.

2.2.1 The visual pathway

Visual information is directly transduced into neural signal by the eyes, where specialized neurons on the retina effectually convert photons into action potentials in the central nervous

system within a few layers of neurons. In a simplified walkthrough of this pathway, photoreceptor cells (i.e. rods and cones) connect directly to bipolar cells, which in turn connect to ganglion cells that transmit the signal into the optic nerve as action potentials [41]. Naturally, the receptive layer is the most populous one, so the receptive fields of ganglion cells consist of increasing numbers or photoreceptor cells. These receptive fields are organized in two concentric circles of the visual map, which serves to discern contrast rather than absolute luminance: neurons can either respond to on-center (inner area brighter), off-center (outer area brighter), or on-off (change in relative luminance) excitation [42]. The size of the receptive field relates to the spatial precision of sensory data, thus bipolar and ganglion cells in the fovea have the smallest receptive fields for the best visual acuity.

This receptive field structure is retained as the information is relayed along the optic nerve into the brain. The signals coming from both eyes merge in the optic chiasm, and are divided again so that information of the left and right halves of the visual field are transmitted in their own tracts. This causes the typical arrangement of the right occipital lobe processing the left half of the visual field, and vice versa [43].

The lateral geniculate nucleus (LGN) of the thalamus serves as the significant hub along this pathway. It provides the main visual input to the cortex, in addition to relaying retinal information to secondary locations. In the LGN, the visual information is split between two major types of pathways. The magnocellular (M) layer carries rapid information of higher temporal resolution, e.g. about shape and movement, whereas parvocellular (P) cells provide finer details about contrast [44]. The LGN does not only serve as a hub to these connections, but also partakes in processing this information as well as complex circuits connecting several cortical areas [45]. Importantly, it employs attention-based modulation to the sensory data, and thereby receives feedback from cortical areas affecting its output [46, 47].

The primary visual cortex (or V1), which receives the main output of retinal information from LGN, is one of the largest and densest systems of neurons in the human brain. As retinotopy, i.e. information about the position of the projecting retinal cells, is retained throughout the pathway, the neurons in V1 essentially form a map of both retinal surfaces (Figure 2) [48]. However, the structure and functions of these receptive fields are more complex than in the previous parts, as the area participates in initial feature extraction from the visual data and merging the input from both eyes [49]. These systems of neurons in V1 are selective to stimulus shape, orientation and movement direction. The primary visual cortex sends out information to higher visual areas (denoted V2, V3 etc.), which perform various, increasingly complex, functions of image processing such as size, colour and spatial frequency. Notably for the purposes of this thesis, area V5 (or MT) is regarded as the key cerebral module for motion perception [31]. Finally, visual information is certainly a key part of functions other than purely sight – e.g. motor feedback – and the visual areas feed signals to numerous functional areas.

While the hierarchical pathway described above does form a useful model for the major sequence of activation and temporal dynamics (Figure 3), information will also travel via both less populous and more complex paths. Furthermore, these feed-forward pathways simply enable the passage of sensory information towards various functional areas, as opposed to reflecting cognitive processing. To modulate this processing in the higher visual areas, they in turn connect back to the primary visual cortex, which consequently has feedback connections to the LGN, resulting in a highly complex reciprocal network when adding the plethora of other

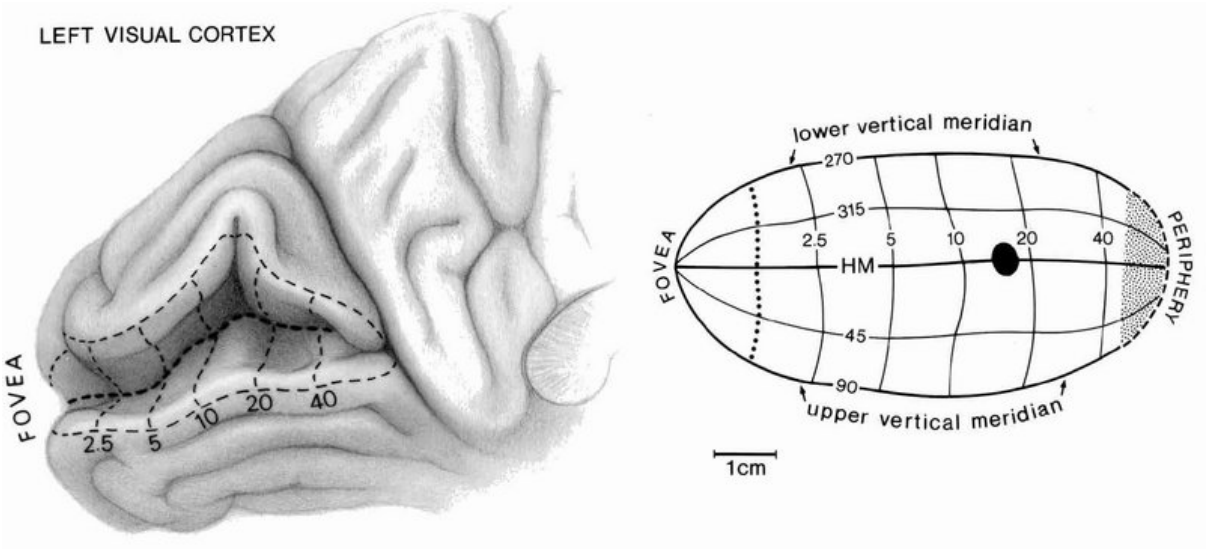

Figure 2 – Retinotopic map on the primary visual cortex, also demonstrating the greater amount of resources devoted to the fovea (image: scholarpedia.com).

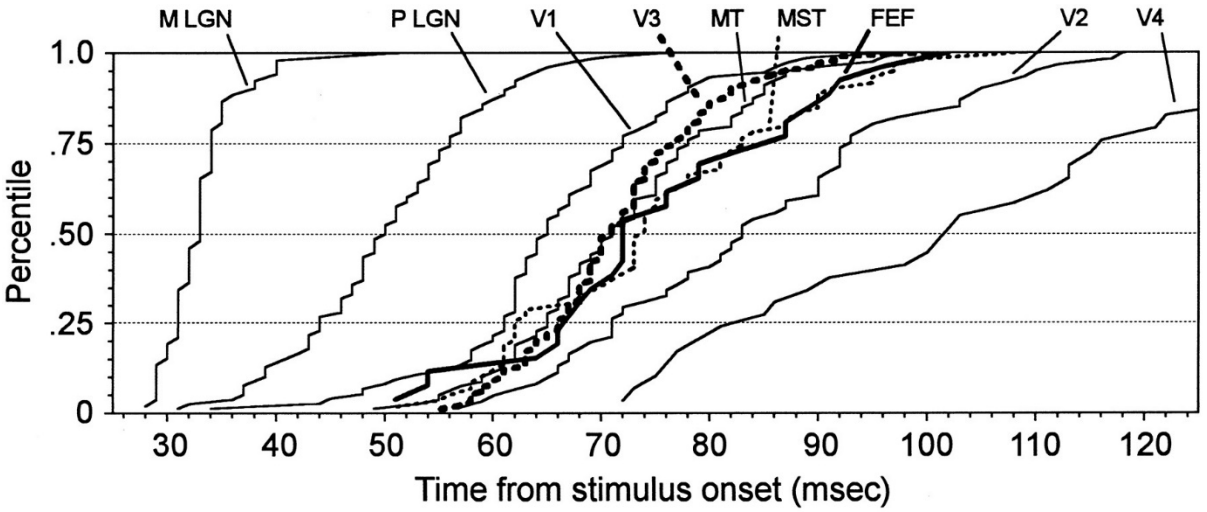

Figure 3 – The percentile of cells in an area responding to a visual stimulus as a function of time from presentation in macaque [54].

connections into and out of area V1. There is also evidence of both higher visual areas such as V5 having more direct connections for rapid signals where the area responds as fast or faster than V1 to a visual stimulus [17]. Area V1 has also been found to participate in more abstract brain functions such as interval timing [50, 51]. Furthermore, the cortical areas in charge of eye movements such as the frontal eye field (FEF) are heavily connected with the occipital visual areas, and may play a part in both early, rapid processing and higher-level sensory functions such as attention [52]. Thus, while the categorization of cerebral areas and their roles in elementary functions might be resolved up to a degree, the big picture of visual processing as a whole remains convoluted beyond the grasp of the measures reviewed here. Nevertheless, visual phenomena can be analysed via the timing and approximate location of the evoked biosignals, which elucidates cortical functions taking part in the investigated function.

2.2.2 Responses to visual stimulation

Presenting a stimulus, i.e. a change in luminance, will trigger the activity cascade as described above. While the activity is first noticeable in electromagnetic recordings after 50 ms from stimulus onset, most of the purely visual areas reach maximum neural recruitment at around 100 ms. In literature, the waveforms are generally identified by their latency from stimulus presentation. These evoked responses (evoked fields in MEG, and evoked potentials in EEG) vary in their timing, amplitude and waveform based on the characteristics of the stimulus, but typically the responses exhibit at least one positive or negative peak that peaks in this point in time (hence named P100 or N100 etc.) [53]. The sensory areas will remain active for some hundreds of milliseconds, and usually the timeframe for signal analysis extends to about 500 ms from stimulus onset. Within ca. 200 ms, the activation will have spread to multiple brain areas for complex cognitive processing [37, 54].

Out of the later, more complex signals, the mismatch response in an oddball task is a relevant and well-researched one. In this paradigm, a repetitive or predictable stimulus is interrupted by an anomaly. In the visual modality, this response is associated with e.g. change in colour, location, orientation, as well as motion direction [16]. The areas that are typically activated include the supramarginal gyrus, the anterior cingulate cortex, and the dorsolateral prefrontal cortex, though there are varying reports of these and several other areas showing activity in these tasks, most likely due to differences in the presented stimuli and recording methods [37, 55]. Investigating this phenomenon has also revealed a time frame of roughly 150 ms, in which the regular stimulus must repeat for a mismatch negativity component to appear in EEG [16]; the authors concluded that the time frame constitutes a temporal window of integration, suggesting that visual information is processed in temporal segments of that size, similarly as in audition. However, the event-related signals comprise merely a part of the overall neural activity, and as discussed above, the event-related activation patterns are often indistinguishable in real time due to all other neural activity. This can be overcome by averaging epochs of the MEG or EEG signal, time-locked to the moment of stimulus presentation, which will attenuate the spontaneous activity and reveal any stimulus-dependant activity patterns.

Another approach to characterizing the recordings is spectral analysis. Oscillatory patterns, the rhythmic fluctuation of excitatory and inhibitory states in a population of neurons, are an important element of brain function. The oscillations are divided into categories based on their frequencies: delta (< 4 Hz), theta (4–7 Hz), alpha (8–12 Hz) etc., up to the gamma band (> 30 Hz). For the other signatory values these waves possess, the amplitude corresponds with the recruitment ratio of EPSPs in a particular brain ensemble, phase consistency describes the exact state of the oscillations with respect to a repeating stimulus, and phase synchrony across brain areas is considered an indicator of communication or common task recruitment between the areas [56–58]. Even though the exact functions of spontaneous oscillations are indecipherable as of yet, it is thought that larger brain networks employ the lower frequencies, and correspondingly smaller networks oscillate with faster frequencies [59]. The occurrence of delta and theta waves in sleep and various stages of alertness, respectively, support this claim as they can be considered to be mechanisms with widespread effects, but at the same time do not necessitate the highest of temporal resolutions. Conversely, the higher frequencies are associated with discrete functions such as reasoning, sensory and motor performance. The

alpha waves are of special interest for the examination of the visual modality, as they principally manifest themselves in the occipital cortex. This oscillatory activity appears to stem from the interplay of thalamus and cortex, and thus propagate through the same pathways via LGN as retinal information [60, 61]. The alpha oscillations are predominant in resting-state recordings, and are modulated by the state of alertness as well as opening and closing of the eyes. Additionally, alpha-band activity is modulated by attention, where it likely serves as a filter to attenuate irrelevant information [62]. Moreover, it has been shown that the state of alpha activity can both affect visual task performance and be affected by visual stimuli.

In visual discrimination tasks, or virtually any nontrivial function, humans do not perform consistently even with identical task parameters, e.g. in the presented experiment, equal visual displacements could both go unnoticed and occasionally be detected by the same subject across trials. Naturally, factors such as mood and alertness, or in other words the current state of the brain, affect how well a subject executes a task. Specifically, several studies have concluded that the state of alpha activity at the moment of stimulus presentation can predict perceptual performance, and thus explain this stochastic property of perception [57]. The prestimulus level of alpha amplitude was concluded to be a significant explanatory factor between detected and undetected repeats in a study using a stimulus with an intensity of subjective equality (50% detection probability) [63]. The results support the hypothesis that the brain fluctuates between externally and internally oriented states, varying every few seconds, which can be observed by changes in spontaneous activity [56]. Lower amplitude of the alpha oscillations reflect an externally oriented state where sensory performance is enhanced and stimulus presentation results in stronger evoked responses. Conversely, higher amplitudes represent internally oriented states, during which performance in the aforementioned tasks is inferior, but consequently improved in cognitive functions such as memory [57]. Similarly, increased prestimulus phase coupling has been documented to correlate with poor performance in visual discrimination tasks and thus may reflect the internally/externally oriented state as well [56].

Comparable analysis on the phase of the prestimulus alpha wave revealed a secondary effect, where visual discrimination was increasingly improved during the positive peak of the phase, however this effect seems prone to much inter-subject and inter-experiment variability and may not be limited to the alpha band [56, 64, 65]. Nonetheless, the detection performance can be improved by promoting the occurrence of phase consistency with a frequency-matched stimulus [66]. Rhythmically presented stimuli with an alpha band frequency (e.g. rapidly changing images) can entrain the brain oscillations, which become phase-locked with the stimulus rhythm, causing further stimuli occurring with the same frequency to be perceived with a higher accuracy [66–68]. The effect is thought to represent the brain preparing itself for optimal handling of the upcoming visual information, and may play a role in selective attention by enhancing the processing of relevant spatial and temporal information [69, 70]. This phenomenon could also in part explain the above mentioned findings on evoked signals arising from pattern mismatch stimuli, as the temporal window approximately matches the alpha band in frequency.

2.2.3 Eye movements

The visual system operates with four primary types of eye movements: vergence movements, vestibulo-ocular movements, saccades and smooth pursuit movements [71]. Vergence

movements align the focus of the eyes to match the target depth, and vestibulo-ocular movements compensate for head movements in order to stabilize the image on the retinas. From the perspective of neuroimaging studies, these two types are less relevant, as a stimulus image in a laboratory setting is generally in 2D form from a fixed distance, and any head movements would be detrimental to recordings as outlined in Section 2.1.

Correspondingly, saccadic and smooth pursuit movements constitute the primary means of searching and tracking visual stimuli. Hence, investigating their characteristics are vital for interpreting gaze recordings. Saccades shift the gaze direction between targets in rapid movements (peak velocities above 500°/s), which normally occur between fixations where the gaze direction remains relatively stable. The fixations typically last for 200–350 ms, depending on the observer's task (e.g. reading, visual search, free-viewing) [72]. During fixations, small involuntary movements called microsaccades also occur, which are, in accordance with their name, functionally similar to saccades but smaller in magnitude (under 2°). The purpose of microsaccades is not entirely clear as their characteristics make them a challenging research subject, but they are thought to play a role in counteracting neural adaptation to a static retinal image, and reflecting attention [36, 73]. Smooth pursuit movements allow the observer to follow a moving target more precisely than a sequence of saccades, which is achieved by matching the retinal speed of the target with a continuous movement of the eyes so that it remains in the fovea [74]. Humans are capable of tracking targets up to speeds of 30°/s [75]. Curiously, despite being voluntary movements, they require a target to be invoked, as can easily be tested by attempting to produce them while looking at a blank wall.

Both smooth pursuit and saccadic eye movements involve a wide cerebral network, as they require a combination of muscle control and sensory information to operate in tandem. Structures in the reticular formation of the pons and midbrain provide the main control of eye movements, while being under the influence of the basal ganglia and cerebellum as for all movements [76]. For saccades, both the superior colliculus in midbrain and the cortical frontal eye field (FEF) appear to function in overlapping and/or complementary roles for the purposes of saccade execution and target identification, and stimulating these areas results in the production of arbitrary saccades [77]. Smooth pursuit movements are likewise controlled by the reticular formation in addition to having several common network nodes with saccadic movements, but the related cortical processing locations differ as the motor control occurs outside FEF for smooth pursuit [76, 78]. However, it is clear that visual information and feedback especially from V5 is a prerequisite to smooth pursuit movements.

The actuation of these movements is performed by the six extraocular muscles, which also serve the function of keeping the eyes in place. The dynamics of saccades resemble that of limb movements in many aspects. Their force–time functions closely match each other, and both movements demonstrate a similar speed–accuracy trade-off, where larger saccades accelerate faster and to a higher peak velocity, but have higher variability in endpoint locations [79]. The results of the referenced study show that saccade groups ranging from 3.0 to 9.0° had endpoint variances of 0.654 to 0.883°, with a linear relationship. Additionally, displacements below a threshold of approximately 0.5° may not elicit a saccadic response [75]. In comparison, individual fixations to a stationary point have been shown to have a variance of roughly 0.1°, which may be used as a baseline noise level in this context [75, 80]. The saccades occur with a reaction time of 150–250 ms from a sudden displacement of a focused object, and muscular movements seize after ca. 250 ms after saccade completion, where the later activity seems to

facilitate the eye coming to rest in its new orientation [75, 81]. In fact, as a difference to limb movements, eye movements lack antagonistic muscle activity to apply braking force and the deceleration is caused solely by the viscosity of orbital structures [81]. Furthermore, saccadic movements are ballistic, meaning the course of the entire event is decided at the onset, with possible corrective saccades occurring after a similar delay from the completion of the previous one [75]. Smooth pursuit movements on the other hand appear to be capable of performing corrections with a better temporal resolution. They exhibit faster reaction times than saccades, albeit with a similar acceleration time, and during smooth pursuit it is possible to produce separate responses to target motion changes only 75 ms apart [74, 75].

Despite sharing purpose and several mechanisms, the systems that generate saccades and smooth pursuit movements are traditionally thought to act independently of each other [74]. Rashbass [75] studied the relationship between the two when a stationary target begins to move horizontally. A simple initiation of steady movement caused a corrective saccade in case the movement velocity was at least 3°/s (absent when 2°/s or less). The threshold velocity corresponds to ca. 0.5° movement of the target during the time it takes for smooth pursuit movements to react and accelerate. Otherwise the smooth pursuit velocity is increased while the target is ahead. When target movement begins simultaneously with a displacement, the smooth pursuit movement starts in the direction of the uniform movement of the target, regardless of the direction of the displacement. Thus, the resulting eye movements may initially draw the fovea away from the target prior to the corrective saccade. This result supports the independent systems theory where target velocity alone governs the smooth pursuit movements, and correspondingly saccades are stimulated separately by its position. Rashbass also administered subjects with barbiturate drugs that specifically inhibited smooth pursuit movements, adding further evidence for separate systems.

More recent studies have since uncovered cases where the two systems do appear to cooperate, especially with high-speed targets, where catch-up saccades occur frequently, or in situations where the movement is more complex [82]. De Brouwer and colleagues [83] expanded on the Rashbass setup by following the movement initiation with a second change in both position and velocity simultaneously, and observed the occurrence of corrective saccades. They found that both position and velocity error are taken into account when triggering a catch-up saccade, and identified the key parameter in the decision as the eye-crossing time, i.e. the estimate on how soon would the target and eye trajectory cross. The results showed that trials with an eye-crossing time of 40–180 ms showed significantly fewer corrective saccades, which essentially necessitates communication between the position and velocity systems, namely saccadic and smooth pursuit, when planning eye movements during smooth pursuit [82].

2.2.4 Eyeblinks

For the visual system, eyeblinks pose a significant hindrance in periodically blocking the main sensory input. However, they serve a vital function in applying moisture to the eye surface, as well as removing or blocking irritants from it. Under usual circumstances and without a specific task, humans blink spontaneously approximately 10 to 15 times per minute [7, 84]. This blinking rate is reduced during tasks requiring visual attention, e.g. visual smooth pursuit or driving a vehicle, and increased by fatigue [84]. Likewise, the timing of spontaneous blinking may be controlled by attentional mechanisms during cognitive tasks such as reading [85, 86].

Reflex blinks on the other hand occur involuntarily as a response to stimuli that could harm the eyes, e.g. a sudden bright light, loud sound, rapidly moving object or somatosensation near the eyes. For research purposes, in addition to simply asking the subject to voluntarily blink, electrical stimulation of the supraorbital nerve or using an air puff have proven to be popular means of producing reflex blinks reliably with minimal intrusion [6, 7, 87–89].

Eyeblinks are elicited by the same cortical oculomotor areas as for saccadic movements, including the FEF and the supplementary eye-field (SEF), although reflex blinks transpire without cortical involvement [88–90]. Based on animal and lesion studies, e.g. the basal ganglia and the superior colliculus are likely involved in eyeblink generation [87]. The facial muscles orbicularis oculi (OO) and levator palpebrae superioris (LPS) are primarily responsible for the motion of closing and opening the eyelid, respectively, with the LPS actively inhibiting eyelid closure between blinks [87, 88]. The entire blink from when the eyelid starts descending to the point it returns to its approximate original position typically takes between 100 to 400 ms [91]. A longer closure of the eyes suggests an episode of microsleep, which differs from blinks as microsleep entails a brief slip into a sleeplike state while the eyelid remains down and stationary, as opposed to a near-continuous movement during blinks [84].

In order to more closely study the mechanical events, VanderWerf and colleagues [88] compared blinks elicited by various forms of stimulation and determined that spontaneous blinks have the longest durations, followed by voluntary blinks, air puff–induced blinks and finally electrically stimulated blinks, in descending order of mean duration. Across all conditions, the down phase duration (closing of the eyelid) remained rather constant and varied less within conditions than the slower up phases (opening of the eyelids). For example, the study reported down phases of 92 ± 17 ms and up phases of 242 ± 55 ms for spontaneous blinks. Furthermore, vertical but not horizontal position of the eyes was found to affect blink duration linearly, with downward-gazing blinks having the longest durations.

Blinking causes distinct eye movements. As a result of co-contraction of extraocular muscles, the eye is pushed 1–2 mm back into the orbit, while also rotating nasally and downwards [91]. Bour, Aramideh and Ongerboer De Visser [87] further examined this phenomenon and identified a dependence on initial gaze position (Figure 4). Their results indicate the eyes moving at similar velocities during the deflection and return phases, but the return trajectory becomes noticeably curved towards the end, resulting in the eyes to finish their return with a slow drift. In their experiment, the eyes moved only approximately 100–200 ms during blinks, with a return accuracy of ca. 1–2°. Thus, the authors concluded that the return to the initial location during the up phase necessitates active contraction of the extraocular muscles to occur, as a passive movement would transpire much slower than observed. Despite the induced eye movements, blinks do not appear to cause substantial disruptive effects to saccadic or smooth pursuit movements in step-ramp motion initiation [92].

However, the role of extraocular muscles, as opposed to elastic forces in the surrounding tissue, regarding the gaze-dependency of the phenomenon remains unclear. Two alternatives are possible: the extraocular muscles are activated similarly regardless of gaze position, and thus the trajectory is a result of passive elastic forces; alternatively, the muscle activity depends on gaze position, in which case information of the initial gaze position must be available during the up phase to actively guide eye orientation back to its original state [87]. The latter hypothesis is deemed somewhat complex for its purpose by the authors, as it requires

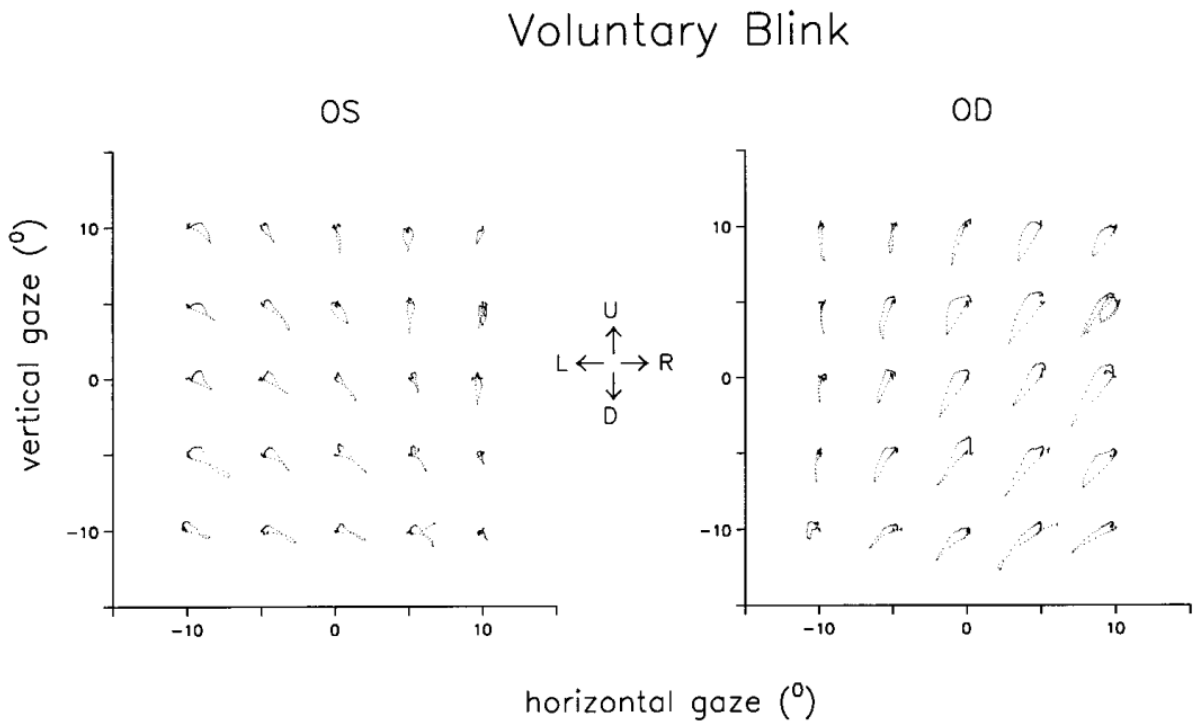

Figure 4 – Gaze direction trajectories depending on initial eye position during a voluntary blink [88].

communication between the neural systems controlling blinks and other eye movements. Nevertheless, several phenomena encompassing blinks suggest that the blink system does engage brain areas additional to mere eyelid movements; there are similar findings regarding saccadic eye movements.

2.2.5 Neural effects of blinking

In addition to the systems responsible for the related motor commands, blinking clearly affects the visual system as the retinal input is momentarily suppressed. In fMRI, blinking causes a sizeable hemodynamic response in area V1, much greater than other eye movements, which is thought to facilitate processing of the significant changes in visual input [36]. Likewise, blinks have been found to evoke post-blink activity in parietal areas associated with change awareness, possibly a sort-term memory that supports the maintenance of the perception of the scene [93, 94]. Moreover, thusly localized activation did not appear when blinks were elicited in darkness, i.e. there was a lack of stimulus to be maintained, implying that this activity was indeed related to visual memory [94]. However, another study observed suppressed activity in parietal and prefrontal areas, which were similarly interpreted as affecting awareness [8]. Elsewhere, a model for reverberatory visual memory via the cortico–thalamic loop between V1 and LGN has also been proposed [15], leaving the question open on how and where visual memory is maintained across blink- and saccade–related gaps [95].

2.2.5.1 Blink suppression

The most pronounced effect of blinking is the suppression of neural activity in the visual cortex, exceeding the reduction in activity expected from the change in retinal input [96]. In primates, the blink suppression effect was studied in comparison with a mimicking external darkening and the disappearance of a target stimulus [6]. Single-cell recordings (measuring the firing of

individual neurons) from area V1 revealed that compared to the baseline, all conditions caused similarly lowered firing rates, yet the effect was strongest for blinks, followed by the external darkening condition. In man, the blink suppression effect was found to occur similarly in situations where retinal stimulation was kept constant via an oral light source [8]. In a follow-up study in primates, the authors confirmed a comparable effect also present in the secondary visual areas that applied to saccades as well, however, they also identified a minority population of neurons that presented significantly varying responses based on the stimulus condition [97]. Further research has suggests that blink and saccadic suppression arise from the same mechanism as the magnitudes of suppression are comparable, stimulus properties affect perception similarly, and the beginning of suppression precedes the movements themselves in both cases [9, 36].

The suppression phenomenon likely explains why blinking is barely perceived despite its considerable effects to vision, in addition to the poor performance in visual discrimination tasks across blinks and saccades [7, 10]. For example, the ability to detect a change in the brightness or contrast of a steady light source decreases by roughly 0.5 log units across blinks [7, 9]. Spatial discrimination, specifically identification of the direction of a 0.71° displacement, was also shown to diminish when disturbed by a blink (80.4% vs. 87.4% success rate in no-blink–condition) [98]. Curiously, this effect can be attenuated by the so called blanking effect, where for a brief period following the blink the stimulus is not shown at all [95]. In the aforementioned study, introducing the blank improved the detection of displacements (65.4% vs. 54.3%, experiment design slightly differs from the former results) [98].

O'Regan and colleagues [12] examined the discrimination performance with more realistic images, showing e.g. people in everyday situations, wherein they would introduce changes, such as altering the relative position of objects, during blinks. Their results indicated, as expected, that changes to central picture elements and those that were being focused on prior to blinking were most easily detected. However, changes to near-focus (within 1°) elements were detected in merely 60% of the trials. The authors concluded that not all the aspects of an object – even an attended one – are actively processed or stored across blinks. In addition to the effects on visual discrimination, blinks have been reported to hamper performance in iconic memory tasks (in this case: recall of a previously presented letter array), which may be caused by blinks suppressing related visual information processing in V1 or the more widespread blink-related activity disrupting higher-level processes [99].

2.2.5.2 Fill-in mechanisms and visual stability

The ability to discern whether perceptual changes have happened during disruptive eye movements or diversion of attention are not functionally as important as being able to make use of the new information. O'Regan and colleagues did note that similar blindness to inexplicable changes has been encountered even with no eye movement obstruction, which may be a result of the brain using the immediately available sensory representation of the outside world as the most reliable information [12]. Outside a laboratory setting, continuity of events is seldom breached, and thus it is no wonder that to maintain a continuous percept, the brain fills in information into the sensory gaps. While interpreting scenes as diverse as real-world situations involves higher-level functions than those studies in detail here, it also presents another way of looking at the above results of visual discrimination [11, 100, 101]. Especially for the visual modality, there are plenty of classic examples even of static images where the subjective perception differs from what is objectively present (Figure 5).

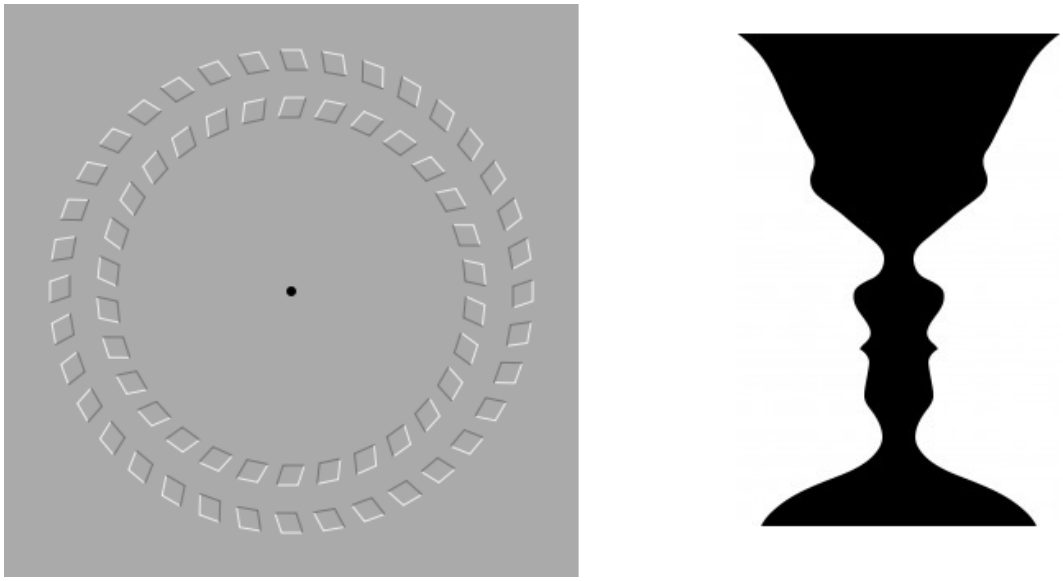

Figure 5 – Examples of illusory images. Left: focusing on the dot, the circles appear to revolve as the viewer moves (image: wikipedia.org). Right: Rubin vase, where the perception switches between silhouettes of the vase and two faces. The shift in perception can be traced at a neuronal level [101] (image: tumblr.com).

The fill-in mechanisms exhibit themselves clearly and persistently in people with scotomas, areas of diminished visual acuity, who are known to experience nearby patterns spreading out to cover the scotoma. Furthermore, these scotomas can be produced temporarily: Ramachandran and Gregory [11] were able to induce them with a stimulus consisting of a static square in a background of twinkling noise. After a brief steady fixation, the square was perceived as vanishing into the background, with the twinkling noise filling in the area. Not only was the sensation of this movement in the manipulated area peculiar, but the effect was also present if the background consisted of English letters, although subjects were not able to read the filled-in letters. Additionally, the vanished area was still being processed at some level, as evidenced by a sensation of movement if a new square was introduced proximal to the location of the scotoma-inducing one. The authors postulated that the fading effect occurs in visual areas processing form (and even separately for colour and shape), independent of the motion perception in area V5. Nevertheless, their results suggest that the fill-in sensation is caused by active mechanisms creating neural representations of the filled-in patch, and therefore continuity. [11]

Similarly to scotomas, the visual suppression accompanying blinks and saccades can be interpreted as a temporary rejection or inhibition of substandard retinal information, as the rapid nature of these interruptions and movements would probably result in sensations resembling photographs taken from a moving vehicle with a slow shutter speed [102]. The similarities between blink and saccadic suppression stated in the previous section imply that the process cannot rely solely on retinal information. Comparing the perceptual effect of blinks and extended eye closures reveals that the impairment relates specifically to eyelid closure and is less pronounced when the eye is simply opened from rest [103]. Furthermore, single-unit recordings have revealed that retinotopic cells in primate brain shift their receptive fields pre-emptively just before saccades, so that the usual retinal field of view of the neuron is restored as the eye catches up [104].

These results are explained by corollary discharges, i.e. motor commands are copied and relayed to the visual cortex [105]. The corollary discharges would then be used to pre-

emptively shift receptive fields and filter the anticipated poor retinal information during the movements, which is all supported by research isolating the eye movements and the motor commands [95]. Corollary discharge, visual masking by peri-movement visuals, and active filling in of the transient scotoma are thought to compose the main mechanisms behind saccadic and blink suppression [9, 15, 95]. Similar mechanisms are documented in limbic control and in the processing of various senses modulated by motor activity in fauna [7]. Additionally, corollary discharge offers a plausible explanation of the blanking effect: if the object is present post-blink, the perceptual system will assume nothing drastic has happened for the sake of stability; if the object is missing, extraretinal information and memory of pre-blink target position are employed to determine its position, thus a different position on reappearance will be noticed [98]. It is also been suggested that the memory component further necessitates a visual stimulus, contrary to the activity suppression effect, as related activity in the posterior parietal cortex is not evoked in darkness [94].

In addition, saccades cause further flaws in perception in both time and space, neither of which occur with eyeblinks or interact with e.g. audition [106]. Time intervals spanning saccades are perceived as significantly shorter, and distances between objects appearing before and after saccades are likewise underestimated and the objects are systematically mislocalized [73, 106]. This spatial compression probably stems from the shifting receptive fields, and from the asynchronous manner in which neuronal populations perform this remapping [95]. Temporal errors, on the other hand, may result from the perceived gaze direction changing prior to the actual saccade [107]. This also leads to subjects erroneously reporting display changes triggered during saccades as occurring prior to them [10, 107]. One hypothesis posits that the brain extends the visual perception back in time, which would consequently increase the subjective postsaccadic duration [100]. However, other research refutes the idea that the "lost" time is recovered, and thus suggests this chronostasis effect is related to movement and attention rather than to time perception [106].

While corollary discharges are central to the creation of visual suppression, which is the most crucial element here, visual stability as a whole takes advantage of other forms of extraretinal information as well. For example, not all retinotopic neurons undergo saccadic remapping, but rather are subject to modulation by eye position (i.e. gain field neurons), most notably in area V1 [95]. Furthermore, not all information is processed in the retinal coordinate frame, hence humans seldom tend to think or navigate purely in those terms. Various areas in the parietal cortex contain neurons that appear to respond selectively to stimuli in a particular area of the visual space, whether it be self- or allocentric [95, 108, 109]. These different reference frames are likely crucial for combining multimodal information, planning movements and interpreting the world as a stable entity, but in a system presently beyond the grasp of scientists [108].

2.2.6 Motion perception

So far, most of the findings reviewed in this Thesis have focused on static visuals and/or discrete changes in stimuli. Nevertheless, it was established that tracking an object employs a specific mode of eye movements to the aforementioned cases, and that visual area V5 appears to be chiefly responsible for processing – and creating a sensation of – visual motion. Motion processing in general does activate a wider network of brain areas: shared activation patterns in comparison to hearing (the other sense humans can use for motion detection) include areas

in the lateral parietal cortex, lateral frontal cortex anterior midline and anterior insular cortex [110].

Compared to saccades, the smooth pursuit mode seems to possess a high temporal resolution, and coincidentally humans perform remarkably well in tasks that not only demand precise interpretation of motion but also produce limb movements to coincide with the target motion. Nowadays, the best examples of challenging motion perception tasks may be found in sports such as tennis or cricket, where the ball can be traveling at speeds well above 100 km/h. A top player can still fairly reliably time his or her bat swing within mere milliseconds for a clean hit, not to mention the strict temporal and spatial requirements for producing the muscle movements [111]. The inherent delays in the passage, processing and sending of information poses an additional challenge in executing such demanding tasks. From stimulus presentation to movement actuation, the reaction delay varies based on modality, e.g. ca. 200 ms in vision, ca. 150 ms in audition and touch [112]. For a discrete stimulus this delay is inevitable, but a task requiring a precise action at a certain time based on continuous movement has the advantage of using prior sensory information (i.e. the trajectory of the target) for preparation. Thus, the accuracy described above necessitates that anticipatory mechanisms are utilized in these scenarios. The flash-lag effect provides a curious example: if a discrete and a continuous stimulus are synchronized, it is perceived as if the discrete one trails in phase [112, 113].

The prediction of how the movement of a visual object evolves is not only based on the immediately observed behaviour, but also on an internal reference model of expected dynamics. Zago and colleagues [14] observed the strength of the prior models in a task where the subjects would intercept a vertically moving target. This proved to be markedly challenging, as the subjects seemingly continue to assume a gravitational acceleration of the target in its absence, and training with the zero-g kinematics merely led to an adaptation of a delay into the model rather than switching it off. Additionally, this behaviour was strongest when the response function was to touch a hidden actual ball in response to the desired interception, as opposed to a mouse click response, where the lack of acceleration was easily accepted. This was found to be in line with previous findings on interpreting virtual vs. palpable object motion. [14]

In other experiments simulating ball-catching – without tampering the dynamics – the subjects are able to time the interception rather well even when the object is selectively occluded, meaning the motor movements had to be planned at least partially based on the internal model of the target motion [13, 114]. The performance did depend on the duration and timing of the occlusion, so that longer periods of invisibility (here: 200 to 600 ms) and occlusions near the "impact" decreased interception success [13, 115]. Furthermore, the total time the target was visible did not have a clear effect, as long as vision was not impaired to the point where subjects had difficulties in integrating brief patches of visual information considerably separated in time [114, 116]. This disruption was likely severe enough to inhibit the generation of an internal model of motion.

The prior expectations can also be modified in a lasting or temporary manner. On one hand, a local visual adaptation to a fast-moving stimulus can reduce the perceived duration of following stimuli [109], and on the other hand the effects of training in a discrimination task can endure for months [117]. Laboratory-bound experiments have mostly had success in showing learning effects highly specific to the task, although training in perceptually challenging exercises such

as video gaming have shown more generalizable improvements [118]. The visual prediction seems to manifest itself specifically on the leading edge of an object, where contrast sensitivity and thus target detectability is increased [119]. Moreover, the effect extends to the interference of spatial patterns of a moving object and a leading-edge target, where the detectability of the target is determined by the superposition of the patterns [119]. The forward-affinity of the prediction may explain the result of another ball-catching study where the occlusion was combined with a preceding change in target speed (decrease, no change, or increase), in which case the speed condition, especially a decrease, produced greater errors in the interception task than subsecond changes in occlusion [13]. Additionally, the accuracy of the speed measurements themselves increase with target contrast, and conversely decrease with movement speed [120]. The latter result, the variability in perceiving a property is proportional to the magnitude of said property, is well documented in most psychometric measurements (i.e. Weber's law) [121].

The perennial favourite ball-catching experiment has been investigated further with the help of MEG, in order to identify the cortical activation patterns occurring during the performance [31]. The study discovered not only a rapid propagation of signals in the dorsal visual pathway that reached from the occipital cortex to sensorimotor areas (that presumably control the related catch movement) in just 40 ms, but also close and overlapping peak latencies in V1 and V5, which suggests a more direct route to V5. This hypothesis is further supported by experiments where transient TMS was applied on V5 at specific times to disrupt motion processing [1]. TMS-induced motion blindness was found to be most efficient when it was applied either ca. 40 ms prior to a motion stimulus, at or near its onset (roughly –20 to +20 ms w.r.t. onset), or ca. 100–200 ms after the onset [17, 122]. While the early effect can be attributed to interrupting preparatory functions, the effect of zero-latency stimulation should be too early to interfere with signals arriving from V1 (see Figure 3), thus hinting towards a more direct LGN–V5-pathway of some kind [17].

Even though the above suggests a rather specialized system that performs its task with precision compared to saccades and static stimuli, motion perception is subject to illusory perceptions of its own as well. A common experience might be standing on a railway platform between two trains, and not being able to immediately identify which objects are actually moving. This likely relates to visual reafference, i.e. interpreting large-scale visual-field movement as self-motion, but with conflicting information in this scenario [95]. Filehne illusion is experienced during smooth pursuit movements across a stationary background, which is perceived as moving in the opposite direction as the target, e.g. observing nearby landscape compared to distant scenery on board a train [123]. Aubert-Fleischl effect relates also to smooth pursuit, and it denotes the effect of perceiving a followed stimuli slower than when fixated elsewhere [124]. These illusions could be explained by motion-sensing neurons having similar centre-surround receptive fields as other visual neurons, e.g. leftward movement in the centre of the field is excitatory, but inhibitory in the surround [125]. Additionally, the model proposes that the motion processing area likewise receives motor information – not just from eye movements – via corollary discharges, which could explain experimental findings where different movement conditions (here: stationary treadmill walking, regular walking, and passive transport) all affect the perception of speed [126].

2.2.7 Monitoring gaze direction

Eye movements seem to fall into few well-defined categories of distinct properties, thus easing the interpretation of experiment-related recordings. However, exceptional temporal as well as spatial resolution are required from the recording method, over a large dynamic range: the movements can shift eye position greatly, yet the precise position is still of interest. This is particularly true in the experiment of this Thesis, where the information is applied partially in real time. Three methods have proven themselves useful in this regard: video-based tracking, electrooculography and scleral search-coil methods.

In the main experiment of this Thesis, a video-based tracking device is employed. This increasingly popular methods is based on real-time monitoring of the eye with a camera, and determining the eye position from – commonly – the corneal reflection [127]. An algorithm extracts the features of the pupil and the reflection from the video images, and determines gaze location by comparing these to the calibration data [128]. By employing infrared light for the tracking, its distracting effect on the subject is further minimized, as well as enhanced pupil–iris contrast [127]. In addition, the device does not require any physical contact with the subject, and as such is the least invasive gaze direction measurement method. Furthermore, modern equipment are able to produce exceptional spatial and temporal resolutions, e.g. the SR Research Eyelink II used here reports 0.01° RMS resolution and <0.5° average accuracy [129]. The disadvantage of video eye tracking is that the observed gaze direction is in essence indirect, and thus only as good as the algorithm backend. Situations where the feature extraction fails, e.g. eye closure or gaze direction beyond the limited calibration range (Eyelink II reported a range of 36°), would produce similar unquantifiable output, which somewhat limits the applications.

Electrooculography (EOG) greatly resembles EEG, and only differs in electrode placement, hence possessing similar key properties. The main signal of interest in EOG stems from the corneo–retinal standing potential, causing eye movements – equivalent to a moving dipole – to induce a detectable signal on the electrodes. The excellent time resolution is combined with a wide spatial range not inhibited even by eye closure. However, the EOG signal and true eye position correspond nonlinearly, increasingly so with larger ranges of motion, limiting the spatial accuracy to approximately 2° [130]. The nonlinearity is caused by conduction through nonhomogeneous tissue, relative movements of the eyelid, and confounding extraocular muscle activity, to name a few [130, 131]. Thus, EOG presents a reliable way of detecting major events such as saccades or blinks in an easy and inexpensive manner, but fares worse for documenting detailed events. Furthermore, the skin-contact electrodes present a small increase in invasiveness over video tracking.

The scleral search coil, however, presents the most invasive and cumbersome alternative. A fitted contact lens with a slight suction and containing a small coil is placed on the subject's sclera and cornea. With the addition of a local magnetic field, the induced voltage in the search coil reflects eye movements. Historically, the method has provided tremendously accurate information about eye movements with ca. 0.08° accuracy, 1-ms or better temporal resolution, and a range of roughly 30° (varies by design) [81, 130]. However, the cost and potential hazards involved have led to the preference of the former methods in gaze recordings, especially as the increased available computational power has facilitated video-based monitoring.

2.3 Perception of time

Now, an astute observer might note that, according to elementary physics, a judgement relating to the position of an object in a spatially encoded system, necessitates the measurement of time in some way in order to estimate the speed of the object. However, time represents a peculiar metric as the sensation is not sensory but generated in the brain, and the exact mechanisms and areas that produce the sensation remain elusive to date. Here, it will be shown that the observer's assumption of the relation of time and speed estimation is not necessary, and that timing of visual events may arise implicitly from sensory and motion processing.

2.3.1 Performance in time-perception tasks

In comparison to what has been established about motion perception and motor behaviour, humans perform surprisingly poorly in explicit timing tasks; precision of interval estimation ranges from roughly 5% up to 60% of the interval length [3]. The performance also greatly depends on the magnitude of the duration, in a fashion that only follows Weber's law in the time range from seconds to minutes. For intervals shorter than 0.1 s, the precision is relatively poor and even perhaps systematically inaccurate, while subsecond intervals show a fairly constant variation as a function of target duration, and finally variability increases for durations in the range of hours [2, 3]. On the other hand, anyone with intercontinental traveling experience will attest that the brain has a more defined concept of circadian rhythm, and e.g. expert musicians are able to maintain an accurate rhythm for lengthy periods of time.

Furthermore, the judged duration of a transient stimulus depends greatly on its modality, features and context [132, 133]. For example, in the subsecond range, sounds are generally perceived to last longer than visual stimuli [132]. Increased stimulus size or speed tend to increase the perceived duration, even if the magnitude is symbolic, for example in the case of numbers [133]. Presented with a range of stimuli, a subject will bias estimations towards the mean of the group (also known as Vierordt's law) [134]. The mental and physiological state of the subject both affect time perception, as well as stimuli with possibly emotional content [135]. Finally, even sex may play a role as there are results suggesting men fare better in timing tasks [136].

All in all, these findings make it challenging to assume that a subsecond visuomotor task employs the same mechanism as explicit timing, as the former noticeably outperforms the latter. How the passage of time could be included in neuronal processes – explicitly or implicitly – will be outlined in the following.

2.3.2 Models of time perception – dedicated or intrinsic mechanisms

Historically, a dedicated centralized clock model has been the dominant one for describing how the brain interprets time, which does explain e.g. the role of attention in timing or failing to time events, as well as the seemingly effortless cross-modal combination of temporal data [5]. The cerebellum has been a strong contender for containing the dedicated master clock, although evidence points towards numerous regions being similarly vital to timing task performance [3, 137]. These other candidates include the basal ganglia, supplementary motor area, and dorsolateral prefrontal cortex, while timing-related activity has additionally been discovered in

the insular cortex, the striatum, posterior parietal cortex, premotor cortex, with mixed results in their task-specific importance [5, 35, 133, 135, 137–140].These findings indicate that the dedicated timing system in the brain, single or one of many cooperating systems, is likely distributed across a number of the aforementioned areas [141].

Nonetheless, the dedicated – centralized or distributed – models fail to explain several properties of time perception performance, for example how the timing module extends from subsecond to hour range, why the timing performance varies by duration discontinuously, or why the significant variability due to modality and context exists [5, 142]. This has given rise to wholly different intrinsic models, where timing is innately managed by sensory processes by means of short-term plasticity [135]. In other words, the brain would take advantage of the temporal features of its own processing for implicit timing [4]. The division in interval performance would thus be explained by the limit of this plasticity in neurons, as longer intervals likely employ working-memory processes [5]. The separation of mechanisms is further supported by findings of mediation by different neurotransmitters for different temporal scales [143].

Presently, the intrinsic timing model cannot explain all the facets of time perception as a whole; however, there are numerous findings providing strong support for local, sensory-related timing mechanisms, which can satisfactorily explain how motion processing accounts for the passage of time [5]. Simulation models have shown that a network of neurons can encode an interval as a transient state of the network dictated by time-dependent behaviour of neurons, in addition to behavioural studies yielding results more applicable to an intrinsic model of this kind rather than a dedicated clock [144, 145]. This would explain two findings: explicit timing performance is poor as objective time cannot be retrieved from such a network, and rising activity recorded in sensory and motor areas reflects this process [135, 146]. Importantly, this rising activity has been documented in regions as early as V1 and V5 relating to temporal expectation of a visual event [50, 51, 147]. Similarly, the amplitude of evoked brain activity can predict the perceptual response to a stimulus (here: if a variable interval was perceived as shorter or longer than the control interval) [148]. Taken together with the timing-related rising activity, the model could further explain perceptual adaptation as a corollary to neuronal adaptation of previous stimuli [109, 148].

Thus, it is feasible but not assured that the visual system independently manages time for its needs. For example, one could hypothesize that an internal model of movement in V5 is represented by activity shifting along the receptive fields in a manner determined by target speed and prior expectations.

2.4 Conclusions for experiment design

The review in this chapter introduced several manipulations of a stimulus that affect the subjects' visual perception of it. Displacements of a moving object during blinks was singled out as the research interest for the present experiment, thus a very simple stimulus is used to avoid nuisance effects. By varying the displacement, the rate at which subjects noticed or failed to notice the displacement would conceivably give rise to a psychophysical function, the details of which could reveal which mechanics are taken advantage of in this task.

Based on the review, a low detection threshold likely indicates that motion processing and visual memory are essential to retaining visual perception across blinks. Furthermore, motion perception may cause a directional bias in sensitivity [119]. Conversely, poor performance suggests that fill-in mechanisms dominate in producing visual stability. Additionally, previous findings show that the instantaneous displacement may give rise to a sensation of velocity change [11]. The previously mentioned static direction discrimination task showed a significant difference between blink and no-blink conditions at 0.71°; the detection rates were fairly high for both, indicating the effect pursued here probably exists on a similar scale of displacements [98].

Additionally, the rapid nature of blinks and eye movements introduces two conflicting temporal constraints for an experiment program: maintaining continuous updating of the stimulus and reacting to blinks both fast and reliably enough. A stimulus presented at a high and steady number of frames per second ensures the sensation of movement, but limits the time window for processing between each image update. This processing time is needed for detecting a blink and altering the stimulus before the blink ends. If the change is too slow, the desired phenomenon is missed and the displacement is likely obvious. These considerations have guided the design of the experiment program discussed in the following chapter.

3 Methods

This chapter describes the experiment in detail, in terms of both the equipment used to present the stimulus and gather data as well as the structure of the main experiment program. The focus, as indicated above, will be on the ability to examine brain and behavioural events in their native time scale. The design decisions based on the reviewed theory will be reiterated here, in addition to presenting the means employed to analyse the collected data.

The experiment took place inside a magnetically shielded room, where the subjects were seated in the MEG device, facing a screen onto which the visual stimulus was projected. In addition to MEG, gaze position and blinks were recorded with a video-based approach. The eye-tracking camera was positioned on a bench between the screen and the MEG device. Additionally, the subjects held an optical response pad in their lap in order to perform the experiment task. Subjects were provided pillows to seat themselves comfortably.

3.1 Stimulus and task

The stimulus was delivered via a projector from outside of the magnetically shielded room onto a translucent screen, where the projected image extended a 55x41 cm area (23°x17° visual angle), with a resolution of 1400x1050 pixels and a refresh rate of 60 Hz. The target stimulus was a small white square (side length 10 px, 0.17°) on a light grey (RGB = [128 128 128]) background, and moved horizontally across the screen at a constant speed of 2.0°/s (2 px per frame). The square "bounced" off the on-screen borders, vertical black lines on both sides, by instantaneously reversing movement direction. This ensured the object could be tracked in a fairly intuitive way without discontinuities. The borders limited the horizontal area of movement to 18° of the screen (1100 px) in order to ensure good gaze tracking. The object remained at the same vertical position roughly at the centre of the screen throughout the experiment.

As the subject blinked, the object was horizontally displaced by –50 to +50 pixels (–0.83° to +0.83°) in relation to the expected trajectory, i.e. in addition to the expected 2 px/frame movement. The displacement values were taken from a uniform. The range closely resembled those reported in similar experiments, with the addition of high amplitude backwards displacements effectively moving the object backwards during blinks (Figure 6). There were no blink cues, and the subjects could perform them naturally (inasmuch as the situation permitted) for the duration of the experiment without responding to external events. Subjects were instructed to follow the square and indicate perceived anomalies in the movement by moving a finger to trigger an optical response device. The subjects did not receive feedback about their performance.

3.2 Instrumentation and the experiment setup

We gathered information about the subjects' reactions to the stimulus in three ways: optical response pad for perceptual data, MEG device monitoring neuronal activity, and an eye-

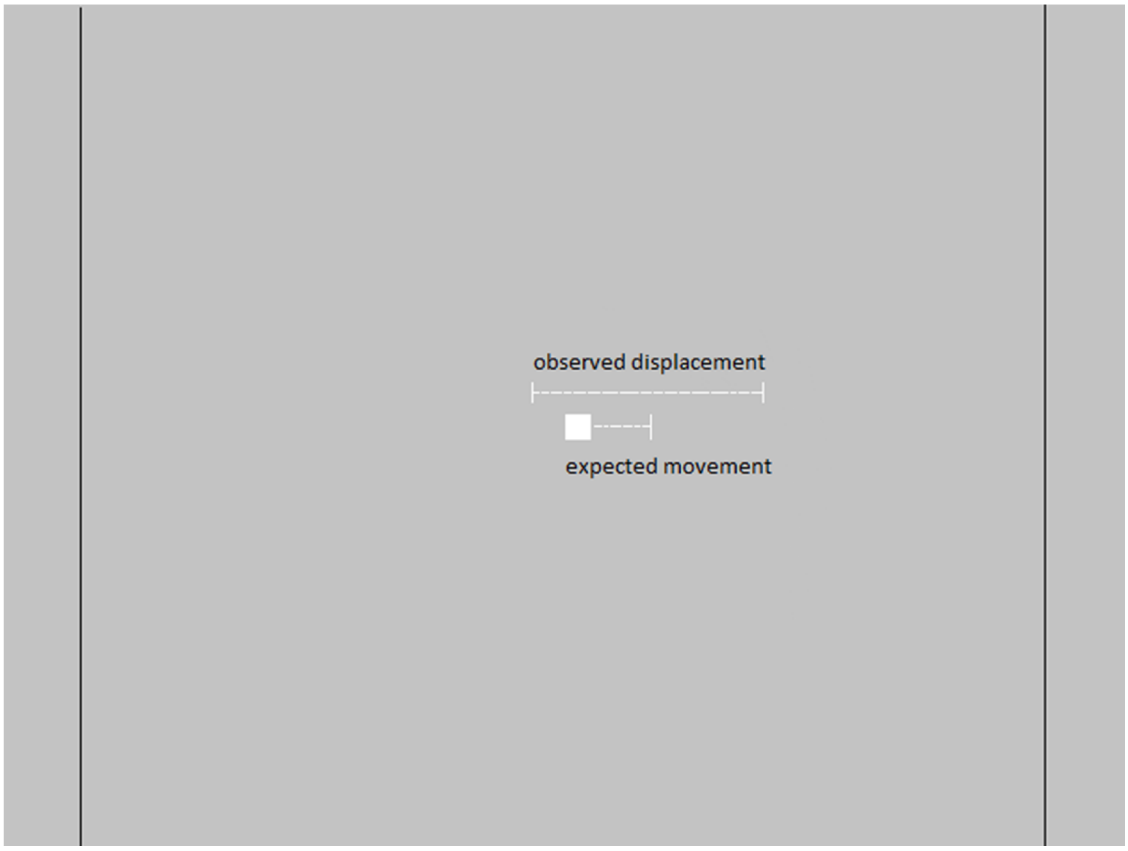

Figure 6 – the visual stimulus (not to scale for visibility) moves across the screen at a constant speed (below dashed line) except during blinks when it is displaced along the trajectory (above dashed line).

tracking camera recording gaze position. The experiment was controlled by a computer (hereby denoted as stimulus PC) that connected all these pieces together as well as sent output to the stimulus-delivering projector. The stimulus PC operated on Windows XP and the computer was quite capable of presenting such an uncomplicated stimulus (3 GHz processor, 2 GB of RAM, and NVIDIA GeForce 8600 GT graphics processor).

3.2.1 Real-time detection of blinks

The eye-tracking camera is controlled by a dedicated computer (denoted as Eyelink PC). The camera, Eyelink II (SR Research, Ottawa, Canada), measures the right eye position at 1000 Hz, in a manner described in Section 2.2.7. The Eyelink PC stores these data at the full sampling rate for post-hoc analysis of eye movements, and also feeds this information to the stimulus PC in real time upon request.

The stimulus PC takes advantage of this gaze information in order to trigger the blink-contingent display change. The stimulus display and controlling of the experiment were produced in MATLAB, taking advantage of Psychtoolbox [149], which has integrated Eyelink support. For practicality, the main experiment program was implemented as a single loop, which necessitates that all functions are executed rapidly enough so that the main loop can keep updating the blink detector and the projected image at 60 Hz, as the smoothest possible target stimulus movement is of paramount importance. Any missed image updates would lead to projected frames where the target does not move, which may hamper the perception of steady movement as well as lengthening the interval between blink checks.

The logic to determine whether a blink is occurring used a similar method as the proprietary software by the eye-tracker manufacturer – if three consecutive samples miss pupil diameter data, the event is considered a blink. From the allotted 16.7 ms per loop passage, this evaluation should then take roughly 3–5 ms. The program would thusly respond to a blink, as judged by the criterion, within 34 ms. Additionally, with a simplistic visual stimulus, this implementation leaves plenty of time to guarantee all other processes such as updating logs and conversing with the other modules of the experiment. Preliminary testing confirmed that the loop processing time, apart from image generation, consisted mostly of the gaze data query function. Furthermore, a detected blink sets a 1.5-s dead time on blink detection, which prevents one blink from being registered as multiple, stops unnecessary blink checking and instead collects target and gaze data onto the stimulus PC event log.

A second response-speed requirement relates to how fast the image subjects see is updated. Constant lag in image production should not exceed the time it takes from blink detection to blink recovery. While display and projector manufacturers can present response times rather dubiously (e.g. grey-to-grey pixel changes), the projector image should have changed within 50 ms from the stimulus PC signalling a frame flip. Thus, even in the worst case of a dropped frame, the object displacement is realized within 100 ms, well within the timeframe of a blink. Unfortunately, there exist no means of determining how close or far from the temporal threshold the program performs in practise, and the violations would only be noticed by subject feedback. However, the timing of blink detection in relation to eyelid movements can be estimated from blink artefacts in frontal MEG sensors, and initial testing showed no signs of delayed visual changes.

Another difficulty arises from the way blinks present themselves in the raw gaze data, since the same ‘no-pupil’ signal is delivered in cases where subjects are looking outside the range of the camera, or if the gaze signal is lost due to an additional cornea reflection etc. Both cases trigger a “false positive” blink, but the latter poses more threat as the subject would undoubtedly notice most displacements not associated with blinks and even change their understanding of the experiment. Thus, the success of the experiment is highly dependent on good calibration of the camera, which additionally improves the precision of gaze data.

3.2.2 Neuromagnetic recordings

The MEG device comprised 306-channels (204 planar gradiometers and 102 magnetometers). The data were recorded with a 1000 Hz sampling rate and 0.1–330-Hz bandwidth. The device has a dedicated channel for triggers, which handily embeds response pad signals into the MEG data file. The stimulus PC also relays the blink trigger to the MEG system, which is likewise added to the measurement data, to allow averaging of the event-related responses. The registered blink onset can vary by approximately 17 ms due to the iteration rate of the main program loop. Additionally, the varying phase where the camera loses sight of the pupil may introduce timing errors. Nevertheless, by having this common fixation point between data files, both the MEG data and the experiment log can be temporally matched by the blink timestamps, and the neural responses can be compared across different conditions. As a redundancy, real-time gaze data (x- and y-coordinates and pupil diameter) from Eyelink was fed to three miscellaneous channels of the MEG system.

3.2.3 Subjects

Six healthy volunteers participated in the experiment. Two of them (including the author) were integral in the development of the procedure and thus informed of research goals and stimuli in advance. Others were unaware of the exact nature of the experiment, but had varying levels of experience of neuroimaging studies in general. The measurements lasted ca. 25 minutes: 2x10 minutes of stimulus presentation, a short pause between the two blocks for the subject to rest their eyes and adjust their position if necessary, and a minute of recording resting-state MEG without stimulation. Preparation comprised of demagnetizing the subject, attaching head position indicator (HPI) coils, seating them comfortably in the device, briefing about the experiment, adjusting eye tracker camera calibration. Altogether preparations took roughly 15 minutes per subject.

3.3 Data analysis

To paraphrase, the experiment produced three data files: MEG data containing neuromagnetic and behavioural responses, high temporal-resolution gaze position data from Eyelink PC that contains high-temporal-resolution gaze recordings, and the experiment log produced by the stimulus program. The latter contains the timestamps for each blink, location and direction of the target at the moment of blink detection, low-temporal-resolution (a sample for each frame) gaze data immediately following the blink (for the aforementioned 1.5-s period), the displacement enacted at each blink and all program variables used for the run. Much of the log information could be used as sanity checks to ensure the program functionality and serve as fixation points to gaze and neural data.

Gaze data are employed in two phases. First, the low-resolution data following each blink trigger is used to manually confirm that a blink was in fact elicited, and that the subject's gaze was on the object (Figure 7). A recovering vertical rise in gaze similar to Figure 4 is evidently seen in acceptable repeats. An automatic approach to the rejection process was attempted, but fine-tuning the parameters was judged to consume more time than manual confirming of blinks, more so considering the recovery range and time after a blink varied between repeats due to variation in camera calibration. Second, the high-resolution data were found to more accurately follow how the eye recovers from a blink and which type of eye movements are elicited to continue smooth pursuit of the target square, and whether they are dependent on the displacement size.

There were no clear a priori regions for the MEG analysis; however, it was clear that the occipital cortex is of special interest. Naturally, blink-locked responses in the visual cortex, and detection-related finger-movement-locked responses in the motor or premotor cortex are expected. By merging the various sources of data, sensor-level signals could be compared between conditions, where differences in signal features should indicate different neural representations of the events. Should clear contrasts emerge thusly, source localization can be attempted, for which purpose some of the subjects had HPI coils attached during the measurement. The detection responses by themselves can be used to model detection frequency of the displacements as a function of displacement value.

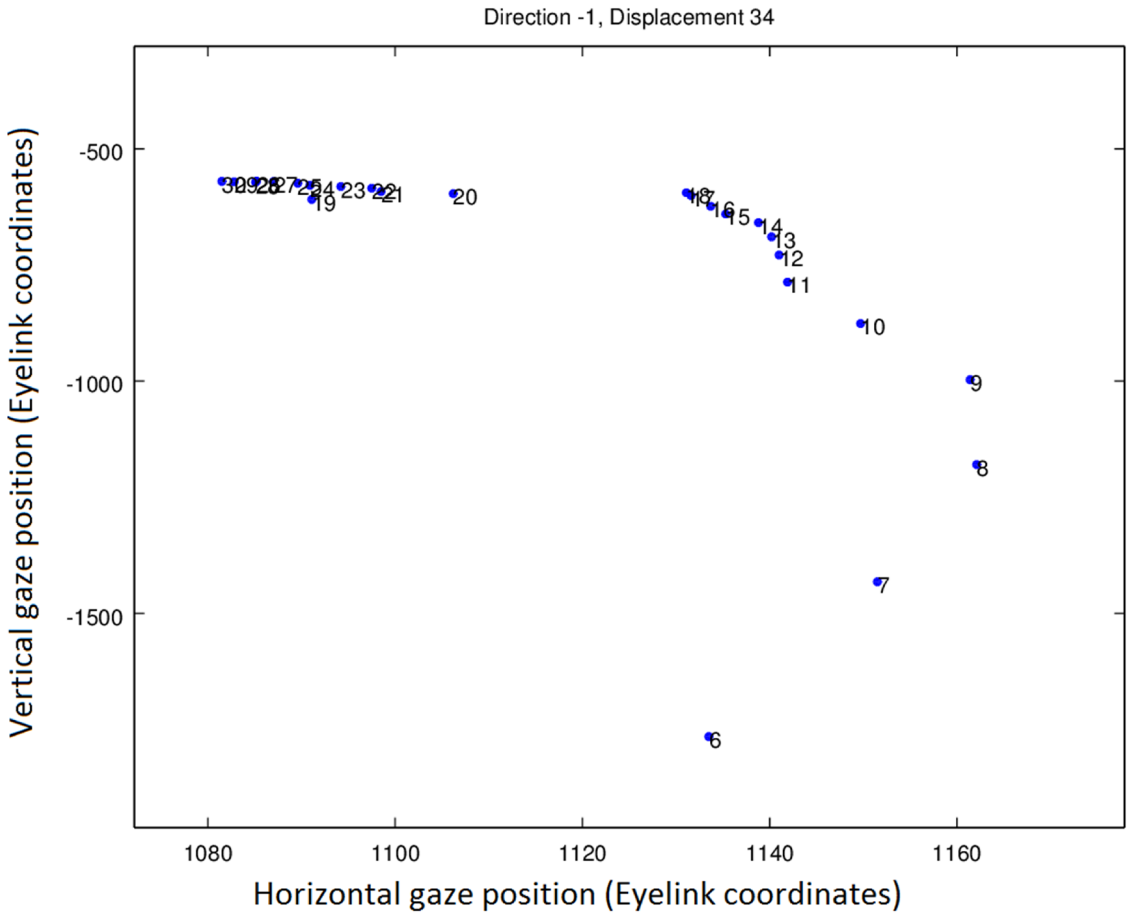

Figure 7 – An example of a low time resolution gaze position data snippet used to confirm a valid blink. The end of the "loop" of blink-related eye movements is evident from samples 6 to 11, as well as the eventual response to the displacement (samples 18–20).

4 Results

Due to the ongoing nature of the experiment, a good number of blinks were recorded in a short time, albeit subjects agreed in that the task felt relatively intense, and some reported fatigue towards the end. In general, the subjects were able to perform the given task well.

4.1 Reliability of real-time blink detection

The constructed program had only four or five frame drops per session – few were expected to happen as a result of the operating system of the stimulus PC and using it with networking enabled. Likewise, all true blinks seemed to trigger the change in stimulus.

Due to the experiment design, a different number of trials was recorded per subject, according to the blink rate. Additionally, discrepancies in subject behaviour and camera calibration prompted a varying number of trials to be rejected. Overall, the rejection rate was low, as only for one subject a significant number of trials had to be culled due to poor camera calibration. This was concluded to be caused by the difference in lighting circumstances between when the camera was being calibrated with the magnetically shielded room open (as the operators had to have access to the equipment) and when the experiment was running with the door closed. Further calibrations were performed by leaving the door just ajar to minimize the effect of external lightning, with greater success. The blink frequencies and rejection rates for each subject are summarized in Table 1.

Table 1 – Blink metrics by subject.

Subject	Total blinks detected	Accepted blinks	Rejection rate (%)	Blinks per minute
1	225	225	0.0	11.25
2	271	263	3.0	13.55
3	270	165	39	8.25
4	68	64	5.9	3.20
5	357	353	1.1	17.65
6	252	252	0.0	12.60

4.2 Discrimination of blink-contingent displacements

While the chosen range of displacements showed reasonable variety from easily detectable to undetectable anomalies for the informed subjects, others reported far fewer, if any, detections. The impact of prior knowledge about the exact type of anomalies was tested by disclosing the details to Subject 6 during a break, which indeed improved discrimination close to the level of the two aware subjects. The individual psychophysical functions, i.e. response frequency as a function of the displacement, are presented in Figure 8.

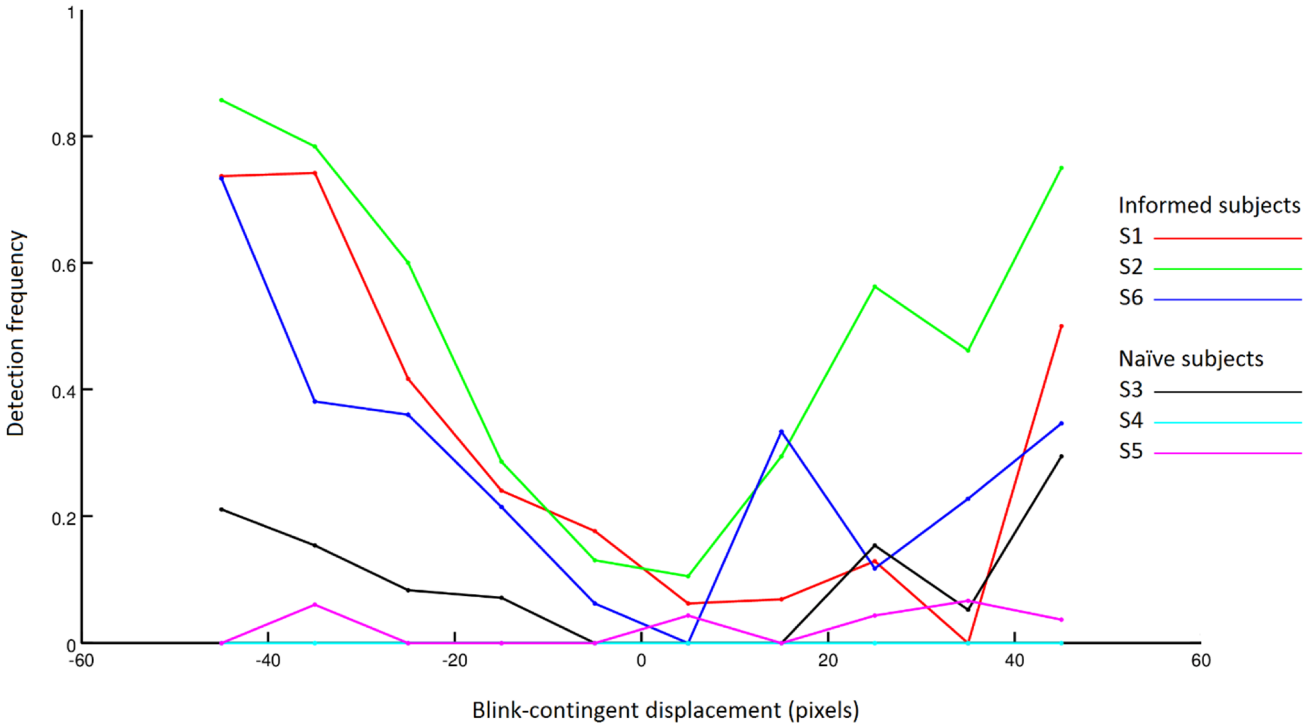

Figure 8 – performance in displacement discrimination task as a function of displacement size (grouped up by bins of ten). Subject #6 reported one detection, to an 8 px displacement, in the first 10 minutes of the experiment. During the break he was informed that a displacement occurs during blinks, and the graph only reflects second-block performance.

In the following, the discrimination rates only for the informed subjects are explored, as within the used range only one of the unaware subjects identified large displacements at a comparable rate. Detection clearly depended on displacement amplitude. Minor displacements (–10 to +10 pixels) were rarely (<20%) detected, while the largest shifts (> 40 and < –40 pixels) were detected several times more frequently. Additionally, large displacements were increasingly detectable if they occurred opposite to the movement direction. Both higher maximum detection rate and earlier threshold for better-than-chance detection related to negative displacements for the three informed subjects.

4.3 Eye-gaze recordings

The eyeball movements accompanying blinks, introduced in Figure 4, closely resembled the recorded gaze shifts of this experiment (Figure 9). While the Eyelink system was able to track blink on- and offset movements to the limits of the calibrated area, the high velocity of these movements did however decrease its accuracy and caused evident jitter especially along the horizontal axis. To combat this, the data were averaged with a three-sample sliding window. Upon closer inspection, the data revealed that the eye did not always return to the original horizontal position and transitioned smoothly from the blink up phase to resuming smooth pursuit (Figure 9). A large displacement elicited slight movements around the expected area of the target and a catch-up saccade to bring the target square to the fovea.

The lower time-resolution data gathered for the stimulus PC could not reveal all the details as prominently, but it provided a good link between the data files, as the timestamping and spatial

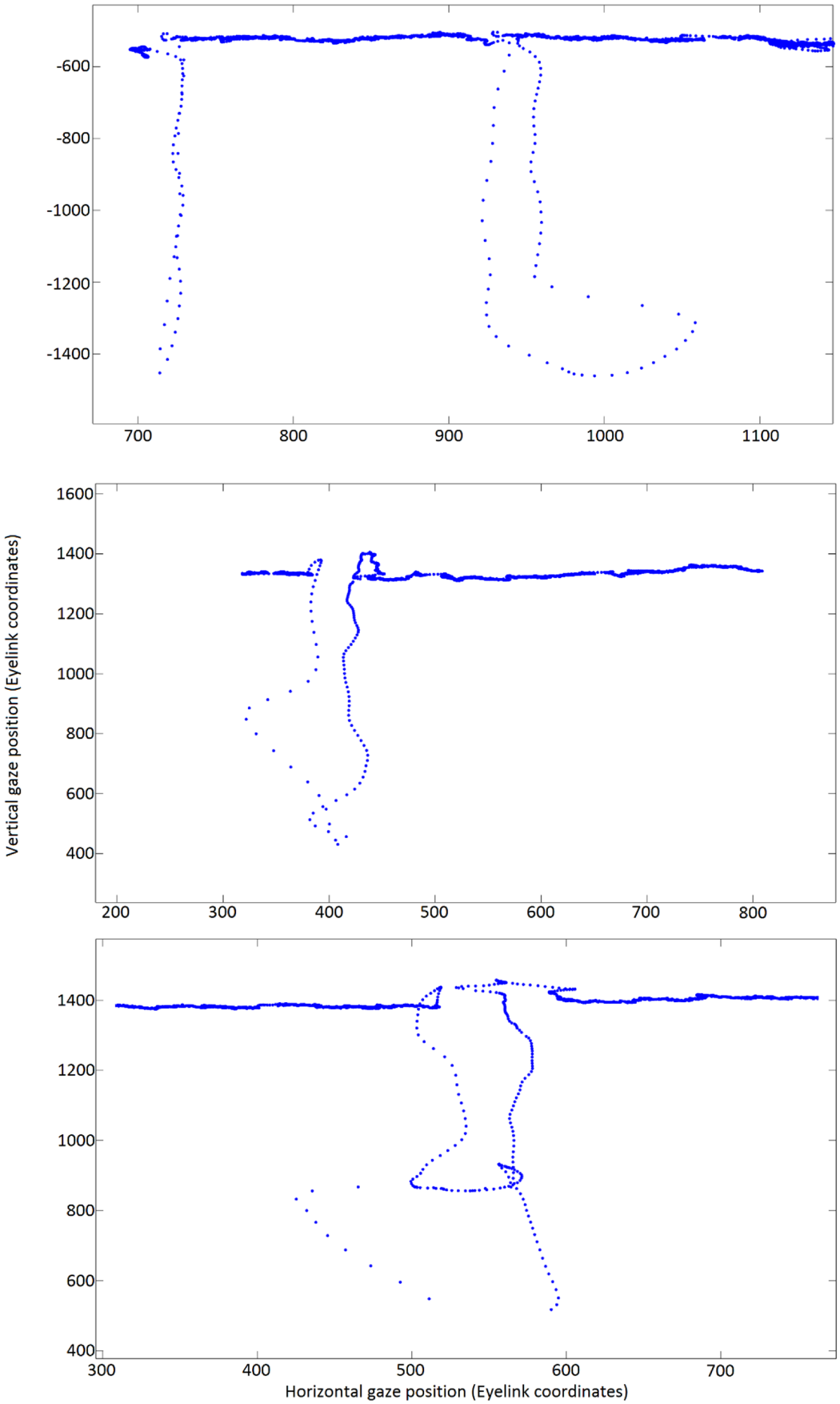

Figure 9 – Top: gaze monitoring showing two blinks during the experiment. Horizontal inaccuracies are noticeable during blink on- and offset movements. Middle: a blink showing the lack of horizontal return to the initial position (object moving rightwards). Bottom: Smooth pursuit seems to return shortly following a blink, followed by a catch-up saccade (object moving rightwards).

coordinates of MATLAB and Eyelink did not match linearly. For identifying well-recorded blinks, the 500-ms samples at 17 Hz fared satisfactorily.

4.4 MEG responses by condition

The recorded neuromagnetic data were pre-processed in order to improve their quality. External noise was eliminated via the signal-space separation method implemented in MaxFilter software (version 2.2; Elekta Oy, Helsinki, Finland). Further attenuation of blink artefacts was attempted with a projection method, however this only suppressed the large spike artefact relating to blinking itself and was discarded. Averaged recordings were smeared by jitter, likely due to the relatively poor temporal accuracy of blink-locking. 40-Hz low-pass filtering eliminated the noise and likely did not affect stimulus-related activity significantly.

Evoked responses in the occipital cortex were compared based on discrimination performance for the three subjects with meaningful detection rates within the used range. Evoked activity from the selected posterior sensors are shown in Figure 10. A relatively high-amplitude oscillatory activity immediately following a blink was evident for some subjects at sensors proximate to the visual cortex. Thus, time–frequency analysis was additionally conducted across all subjects to investigate possible stimulus-induced activity (Figure 11).

As detection, the variable used to group trials here, evidently depends on the size of the displacement, it is imperative to control for the displacement effect separately. The blinks were thus additionally separated between four conditions by both detection (yes/no) and displacement length (long/short, 25-px magnitude limit). The latter comparison was also performed for the subjects whose discrimination performance rendered the first comparison futile (Figure 12).

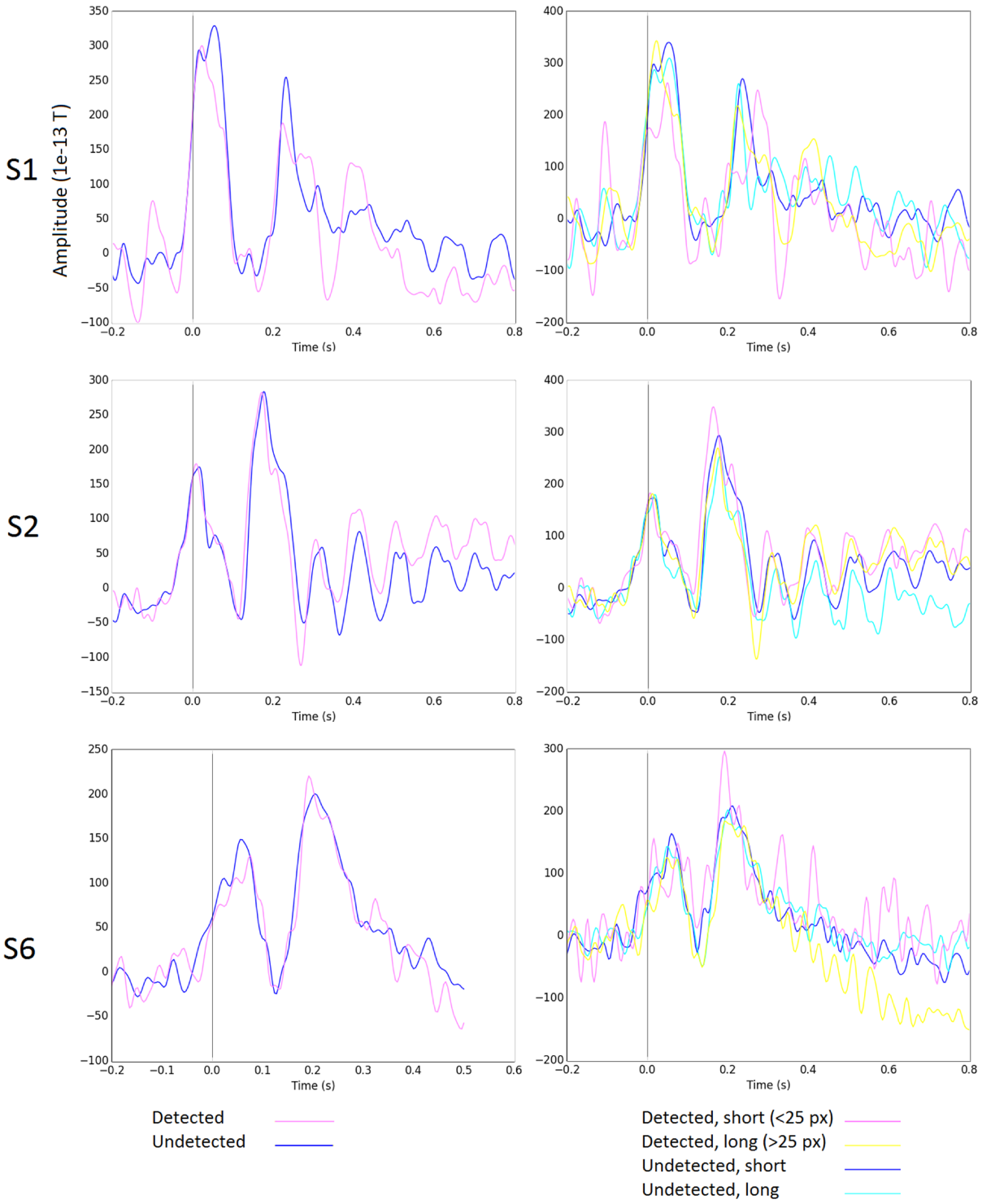

Figure 10 – Blink-evoked responses at a MEG sensor (MEG2331) near the occipital cortex for the informed subjects S1, S2 and S6. Horizontal line at $t = 0$ ms depicts the detection of a blink. Left column: comparison of evoked responses based on displacement detection. Right column: four-way comparison of detection and displacement length.

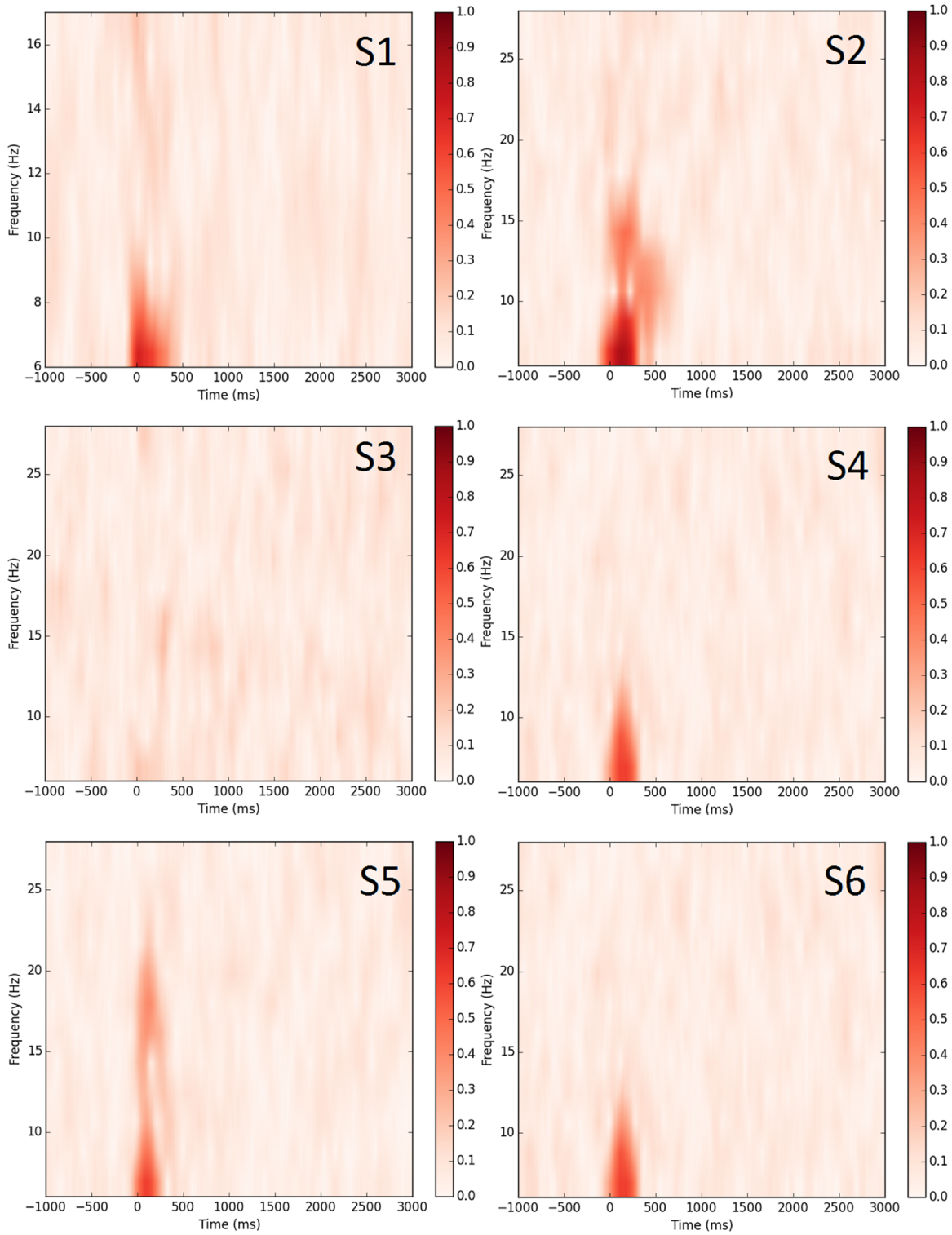

Figure 11 – Inter-trial coherency (ITC) analysis of the selected sensor (MEG2331) for all subjects.

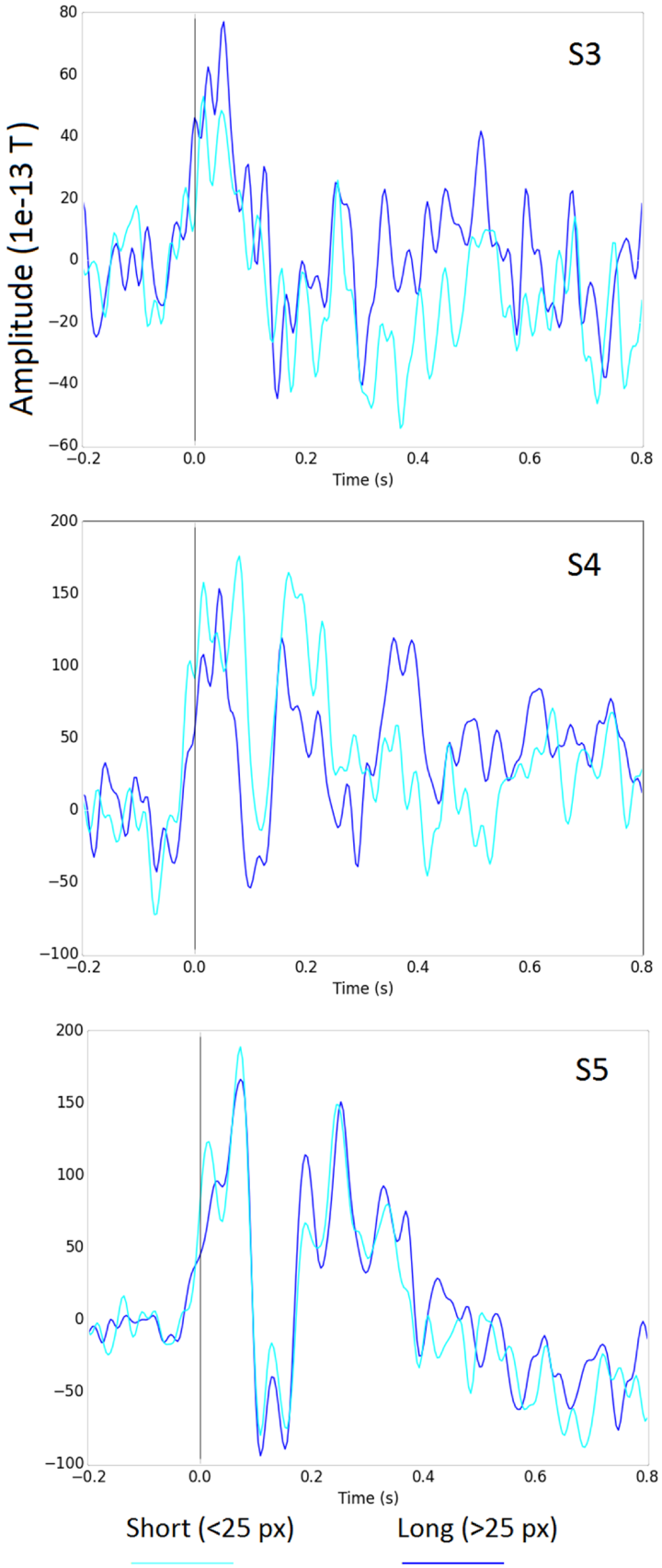

Figure 12 – Blink-evoked responses of the naïve subjects at a sensor (MEG2331). Instead of a detection-based comparison, displacement length was used.

5 Discussion

5.1 Experimental setup and software

Overall, the designed experiment and the devised program fulfilled the beforehand placed goals. Information from all gathered modalities provided useful insight into the displacement scenario in a timescale native to the events. From the program's perspective, everything functioned satisfactorily: blink detection occurred early during the onset, and detection reliability was majorly conditional only to the successful calibration of the eye-tracking camera. However, the false-positive blinks may prove more harmful for a triggered stimulus change lasting more than the single frame update here. In that case, it may be fruitful to devote additional time for the blink registering process. Here, the time demands of computer processing and network communication proved a nonissue, although more coherent timing in blink detection may aid the analysis of MEG data. This could be achieved by transitioning from a single-loop program structure to a dual loop, where the graphics updating would be processed separately to the blink detection function. Thus, a custom-made blink detection module could monitor eye-gaze samples continuously without the risk of degrading the stimulus. Nevertheless, in the present experiment the continuous design in combination with the devised blink detection allowed for expeditious collection of blinks, and the overall rejection rate equalled or surpassed many of the referenced studies.

5.2 Behavioural results

During the experiment, most subjects exhibited a blink rate comparable to everyday situations, with the blink rate suppression anticipated for visually intensive tasks only applicable in the case of Subject 4 [84]. Subject 5 tended to blink at a higher-than-average rate, thus the relatively high blink rate cannot be attributed to any effect relating to the experiment. Nevertheless, it cannot be overlooked that knowledge of the task being triggered by a blink, either by prior knowledge or deduction during the experiment, may have affected blinking behaviour. Similarly, the true spontaneity of eyeblinks can be questioned, especially in the absence of distracting tasks.

The behavioural task revealed two major effects: direction of the displacement w.r.t. motion direction affected discrimination as revealed by the asymmetric psychophysical function (Figure 8), and a priori information about the exact type and timing of anomalies proved imperative in detecting the displacement in the range employed here. The direction dependency implies that motion processing mechanisms, likely in area V5, produce the sensation of discontinuity. Akin to the forward-induced pattern extension [119], one could hypothesize that receptive fields in the predicted path are prepared for the arrival of the target. This kind of prediction cannot practically be binary, rather than a fuzzy logic -type probabilistic prediction, which is supported by the logistical curve of the discrimination function, i.e. a wider area around the predicted location is thusly activated. Furthermore, the most strongly detectable displacements of –40 px or below result in the object being located behind the initial position by the time of blink offset, and are thusly detected at a high frequency. While these findings are convincing, a larger sample size is needed to draw more precise conclusions about discrimination performance.

The inferior task success among uninformed subjects was surprising, especially since displacements in the far end of the range were so reliably detected in the case of informed subjects. However, the results bear semblance to the results of O'Regan and colleagues [12], where even apparent focus on the part of the image about to change did not guarantee the subject observing the alteration. In the light of their findings, prior knowledge may prepare the subject to attend more closely to the specific feature being manipulated, i.e. real-world position of the object.

5.3 Gaze tracking

The recording of gaze direction via the Eyelink camera complemented blink detection by revealing finer details on how gaze direction returns to the focused target after a blink. The final phase of return to the pre-blink direction, was concluded to be promoted by the extraocular muscles [87]. Hence, it is no wonder that this phase was absent if the blink occurred during smooth pursuit, and the muscle activity instead directed the eyes towards the prospective target location. Target relocation being partially fused with blink recovery would explain the low disruptive impact of blinks to intentional eye movements [92].

5.4 MEG responses

Neuromagnetic recordings did not reveal clear trends, as results showed significant intersubject variance. Overall, removing blink-related – but not task-related – activity poses a marked problem which could not be resolved here, making data interpretation relatively challenging. Depending on discrimination performance, the informed subjects did show varying peaks of oscillatory activity in the occipital cortex as well as low-frequency modulation after blink offset. Especially the detected small displacements appeared to cause comparably high amplitude oscillations approximately 200–600 ms after blink detection. This effect was most evident for Subject 2, whereas the neural activity patterns for Subject 6 seemed to vary more by the displacement size rather than detection. Comparisons based on displacement magnitude among naïve subjects affirm its effect on the neural responses within a similar time window. Noticeable inter-trial coherence in the alpha band was documented primarily for Subject 2, which poses a peculiar finding. Similar oscillatory activity patterns did present themselves for other subjects as well, although with seemingly little inter-trial coherence in phase. Conditions inducing alpha-band entrainment were reviewed here, but in cases related to rhythmic stimulus presentation. However, analysing blink-to-blink intervals for all subjects revealed no rhythmic behaviour. It is possible that the estimated 30-ms variance in blink detection due to the single-loop implementation had clouded this phenomenon, and more phase-specific blink detection method is required to investigate it fully.

5.5 Considerations for future experiments

Several unexplored variables remain for the presented experiment paradigm. For example, target speed should increase the uncertainty of the measured speed (by Weber's law), and therefore increase the threshold of displacement for reliable discrimination. The effect of contrast to speed perception could be verified in the current setting, since previous findings suggest increased contrast should narrow the discrimination function [119, 120]. Additionally,

evidence suggests that the magno- and parvocellular pathways of LGN may be dissimilarly suppressed during blinks [9]. E.g. a high-contrast, high-spatial-frequency and low-temporal-frequency stimulus presents information optimally biased towards the parvocellular pathway, and varying these features may affect detectability by differing pathway suppression. Additional simple feature changes, such as size and shape, could very well modify task performance.

Expanding the design beyond the simple object tracking may prove challenging, as smooth pursuit movements profoundly limit other tasks the subject is capable of performing simultaneously. A separate fixation point, or distracting stimuli, could be added, e.g. to examine the interaction of blink suppression and the Aubert–Fleischl phenomenon. However, the task becomes more challenging and complex during blink recovery. Introducing attention into the mix adds a plethora of phenomena to account for. Would unattended objects – which may have just underwent unexpected changes in location – draw the attention, and cause a saccade, unintentionally? The blink-detecting function would have to be more convoluted for practical purposes, at least.

The effect of prior knowledge about the manner of displacement presents a conundrum. It is not clear how examining this parameter should be approached, as investigating a meaningful range of displacements undoubtedly introduces a learning component to the experiment for naïve subjects. The change in perceptual acuity for Subject 6 after disclosing the experiment design was indeed striking, being able to detect displacements within a range that the subject was previously oblivious to. However, a learning effect cannot be reliably controlled by the operators. If the experiment initiates with large displacement trials, the subject may be more attuned to identify smaller displacements later, compared to an opposite order of presentation. It is likely that the subjects here that detected a low but nonzero amount of the displacements could have been attuned to detecting displacements, given additional events with large displacements. Nevertheless, identifying the learning process in time, to compare performance before and after it, is likely impossible unless the ordering of displacements is governed more accurately, or perhaps even interactively.

5.6 Final remarks

All in all, the findings of this research add to the large number of peculiar phenomena related to vision. The behavioural effects discovered are supported by previous results, but they have also shown that unintuitive effects can occur as well. Presently, much technical progress is happening relating to delivering visual content and manipulating devices by visual cues. Augmented and virtual reality displays have seen great economic interest as well, and will likely introduce entirely new ways to manipulate vision and present artificial stimuli for scientific purposes as well. These future methods of stimulus delivery will blur the border between ostensibly simulated and real-world objects, which would help bridge the gap between real-world situations and experiments such as the one presented in this Thesis [14]. However, the more immersive the intended scenario, the more become the critical real-time adjustments to maintain it. While the real-time monitoring to identify select events remained rather rudimentary, the fill-in effects described here could be taken advantage of in order to shroud manipulations of the image without perceptual disturbances.

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